THE INFLUENCE OF LIGHT ENVIRONMENT ON INDIGENOUS TREE SEEDLINGS IN KENYA

by

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MEMORIAL

In loving memory of my parents: Konuche A. Tuei and Tapkesos C. Tuei

DEDICATED

To my wife, Sarah C. Konuche

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF PLATES

ABSTRACT

Attempts to restock large areas of exploited forests in Kenya have been hampered by inadequate understanding on the ecological requirements of indigenous tree species. In particular, very little is known about the responses of these species to different levels of light. This study, therefore, examined the significance of shade and light in regeneration of some important tree species.

The species studied were *Cordia africana* Lam., *Vitex keniensis* Turill, *Markhamia lutea* (Benth.) K. Schum. and *Olea capensis* L. Artificial shading experiments were carried out in the nursery using seedlings of *C. africana* and *V. keniensis*. The effects of different shade levels were compared to full sunlight under low and high nutrient regimes. The response of seedlings transferred among different light environments was also examined. The effects of different levels of light quality (R:FR ratios) were tested. In a forest clearing, seedlings of the four species were grown under artificial shading and their responses were compared to those grown under full sunlight. The influence of deep canopy shade on survival and growth in seedlings of the four species was also determined.

In the nursery, seedlings of *C. africana* and *V. keniensis* maintained positive relative growth rates at irradiance level of 19% of full sun and their growth was enhanced by increasing irradiance. The supply of nutrients at high level also enhanced the growth. Seedlings transferred between light environments acclimated within a month. Acclimation to increase in light availability was faster than acclimation to decrease. Although acclimation was mainly physiological, biomass was allocated in favour of shoots and roots when seedlings were shaded and exposed respectively. The supply of nutrients at higher level had no effects on the acclimation process. Seedlings of these two species showed increased stem elongation under very low R:FR ratio of 0.02, but not at R:FR ratios of 0.36 to 0.65. Seedlings grown at very low R:FR ratio and irradiance level of 12% of full sun showed high mortality when exposed to full sun, but those grown under irradiance level of 19-52% of full sun did not.

In the clearing, growth in height and dry matter production were generally higher under moderate shade in all species except *C. africana*. The latter had highest growth in height and biomass production under full sunlight. High mortality was observed in seedlings of *C. africana* and *V. keniensis* grown under the canopy with irradiance level of 1.5% of full sunlight, but those of *M. lutea* and *O. capensis* persisted for 15 months. Under the canopy growth in height was relatively slow in all the four species. Dry matter production was also low.

The results show that *C. africana* is a typical pioneer species, but the others are intermediate in shade tolerance and are mainly associated with canopy gaps. These results are relevant for rehabilitation of degraded montane tropical forests in Kenya.

CHAPTER 1

GENERAL INTRODUCTION

1.1 THE NEED FOR A BETTER UNDERSTANDING OF FOREST REGENERATION IN KENYA

During the last two decades, there has been accelerated decline in forest land area in Kenya. Annual loss has been estimated at 5000 hectares (Ministry of Environment & Natural Resources, 1994). The remaining closed natural forests now cover about 1.2 million ha and they occur in high potential lands which support 80% of the country's population. These forests are therefore under great pressure from the increasing population.

The main causes of forest depletion are conversion to agriculture and excisions for settlements. The quality of the forests has also declined as a result of uncontrolled commercial logging and extraction of woodfuel for domestic and commercial purposes. Although uncontrolled exploitation has been banned since mid-1980s, this has never been effectively enforced. As a result, recent inventory surveys have indicated that sustained logging is not feasible given the current degraded state of the forests (KIFCON, 1994).

The remaining forests in Kenya have an important role to play in enhancing socio-economic development and protection of soil and water resources. Despite accounting for only 3% of the land area of the country, these forests harbour a large proportion of the country's biodiversity and are therefore important in promotion of tourism, a major foreign exchange earner in Kenya.

Wood requirement in the country for domestic and industrial use has been estimated at 16 million m^3 (Ministry of Environment & Natural Resources, 1994). The country is currently self-sufficient in industrial wood, but woodfuel supply is inadequate to meet the demand. The current population of 25 million people is expected to double in the next 25 years. The requirement for wood is also expected to double during the same period. However, the forest area is likely to decline leading to serious wood deficits and environmental degradation.

To alleviate further degradation and depletion of the remaining forests, a review of the forest policy has just been completed. A new forest policy (Ministry of Environment & Natural Resources, 1994), which is likely to come into effect in 1995, has emphasized the need to manage the remaining forests on a sustainable basis for environmental protection, production of forest products and for conservation of biodiversity. Preparation of the forestry development programmes for the next 25 years has also been completed (Ministry of Environment & Natural Resources, 1994). These programmes include: intensification of farm forestry and related agroforestry to increase wood supply in farmlands; improvement of establishment and management of industrial plantations and improved conservation and management of natural forests. Since many forest areas have been deforested, the programme on conservation and management of natural forests calls for rehabilitation, using more effective natural and artificial regeneration methods.

Past forest policies emphasised on establishment of industrial plantations with fast growing exotic tree species (Kenya Government, 1968). The aim was to increase the supply of timber to meet the needs of a growing population. Because the indigenous tree species were found to be more slow growing than the exotics, they were given little attention in the plantation programme (Logie and Dyson, 1962). However, there has been a shift in favour of using indigenous species to restock degraded forest lands, and areas that would normally be planted up with exotic species. This change has been due to increased risks of attacks of the main plantation species by foreign pests and diseases. During the late fifties and early sixties, two high yielding species, *Cupressus macrocarpa* and *Pinus radiata*, were discontinued from the plantation programme because of their susceptibility to fungal diseases. More recently, two other important species, *C. lusitanica* and *P. patula* have been threatened by exotic aphids.

In natural forests, uncontrolled selection cutting has been practised for many years. This has resulted in occurrence of scattered openings of different sizes. Most areas have been depleted of the best timber species and mother trees (Kigomo, 1989). In the exploited areas, seedlings and saplings of valuable species are absent. The poor regeneration of the valuable species may be related to the amount of light reaching the forest floor. As most of the valuable species are thought to be light demanders, the low irradiance below the remaining trees is inadequate for their regeneration. It is also probable that some of the species are shade-tolerant and the openings or gaps created by selection felling allow too much light in for high survival and successful regeneration.

Since natural regeneration is inadequate, accelerated recovery of the degraded forests will require silvicultural interventions such as reforestation or enrichment planting. Studies by Kigomo (1987) have shown that enrichment plantings can succeed if properly managed. However, there is inadequate information on the light requirements of indigenous species, although limited experience indicates some can be established in plantations. It is, therefore, necessary to investigate the growth requirements of individual species, and especially the responses to different light environments.

In tropical forests, there are very few examples of successful natural regeneration following logging or clear cutting, and the poor regeneration has generally been attributed to lack of knowledge of the requirements of individual species (Gomez-Pompa and Burley, 1991). Light environment is one of the most important environmental factors which influence regeneration processes (Whitmore, 1985). Light influences seed germination, growth and establishment through the effects of different levels of irradiance, light quality and changes in the light availability.

Tropical tree species vary widely in their response to different light environments (Richards, 1952; Whitmore, 1985; Bazzaz, 1991). The response to light generally depends on whether a species is light-demanding or shade-tolerant. This classification is usually based on distribution of tree seedlings in space and time (Whitmore, 1985). Seedlings of the pioneer or light demanding species regenerate in areas open to full sunlight or in gaps, while those of the shade-tolerant species germinate and persist under closed forest canopies for many years (Whitmore, 1985). Some species, however, may be intermediate in shade tolerance. The light requirements of a species may also vary with time. While some species may regenerate in shade, they need full sunlight for good growth as mature trees. The light environment may also vary considerably near the forest floor depending on the degree of disturbance. Changes in the light environment following disturbance are also accompanied by changes in other environmental variables such as the temperature, humidity, soil moisture and soil nutrients. Forest clearings are usually cultivated, grazed or regularly burnt resulting in reduced soil fertility. These factors of the physical environment influence forest regeneration, especially in large gaps and clearings. An understanding of the response of individual tree species to different levels of light (irradiance) is, therefore, necessary for any successful forest rehabilitation programme. The role of nutrient supply may also be important because of the changes in nutritional status of the soils following disturbance.

During logging, seedlings growing below the canopy may be suddenly exposed to bright light. Subsequent growth of weeds may also result in the shading of the seedlings. The ability of seedlings of a given species to survive and grow in response to such changes in the light availability will depend on their capacity to adjust to irradiance and light quality. The increase in air temperature and reduced humidity associated with such changes in the light environment may also influence the response. Studies on the acclimation potential of seedlings can therefore provide essential information for silvicultural management.

Light quality is also important in forest regeneration. Studies on herbaceous plants show that species from open habitats are more responsive to changes in light quality (Morgan and Smith, 1981) and display marked stem elongation under reduced R:FR ratios. In gaps and clearings, rapid growth of weeds may result in the shading out of any regeneration. It is therefore important to study the responses of seedlings to shade light(irradiance and spectral quality).

In Kenya, only one study has been undertaken on the influence of shade in forest regeneration (Kigomo, 1990). The study was, however, based on one species, *Brachylaena huillensis*, and did not investigate the effects of light quality. The possible role of nutrient supply in responses of tree seedlings to different levels of light has not been studied. Furthermore, many species largely remain uninvestigated as about twenty species are likely to be used in the rehabilitation programme.

1.2 AIMS OF THE STUDY

This study aimed at exploring the role of light and shade in regeneration of some valuable indigenous trees in Kenya. The study will provide a better understanding of management of either natural or artificial regeneration in degraded forests. In particular, the study will indicate the suitability of the individual species for planting under full sunlight (e.g. under plantation or agroforestry situations) and canopy gaps of different sizes (e.g. in enrichment planting).

The specific objectives were to determine:

(a) the responses of seedlings of *Cordia africana* and *Vitex keniensis* to different levels of irradiance and nutrient supply under semi-controlled conditions in the nursery;

(b) how seedlings of the above species acclimate to sudden change in the light environment under the above nursery conditions;

(c) the responses of seedlings of the two species to light quality; and

(d) the responses of seedlings of *C. africana*, *V. keniensis*, *Markhamia lutea* and *Olea capensis* to different levels of irradiance under field conditions in a forest clearing and in deep shade beneath a closed forest canopy.

Five experiments, three in the nursery and two in the field, were carried out to address the above specific objectives.

CHAPTER 2

GENERAL MATERIALS AND METHODS

2.1 EXPERIMENTAL SITES

The sites selected for conducting the study were at the Kenya Forestry Research Institute (KEFRI) Muguga and Chuka Forest Reserve. Three nursery experiments were carried out at Muguga Research Nursery while two field studies were undertaken in Chuka Forest. Muguga and Chuka are in the Central Highlands of Kenya but are about 180 km apart. Muguga was selected for the study because of the need for closer supervision of the nursery experiments. Chuka Forest was chosen because the study species occur within the area and access to the forest was good.

Muguga is 01° 13'S and 36° 38'E. The altitude is 2096 m above sea level (a.s.l.). Climatological data for Muguga have been documented by Kenya Meteorological Department (1984). Annual rainfall averages 969 mm. The rainfall pattern is bimodal. The rainy seasons are from March to May and mid-October to mid-December. Owing to the high altitude, the temperatures are relatively low for the tropics with a mean annual temperature of 15.8 °C. The average relative humidity is about 70 per cent. The mean daily solar radiation is 460 cal cm^{-2} (Kenya Meteorological Department, 1984). The solar radiation is low from June to August (Figure 2.1) because the weather is usually cold, cloudy and misty. January to March is usually sunny and dry resulting in high solar radiation.

Chuka Forest is situated at about 00° 20'S and 37° 38'E on the eastern slopes of Mount Kenya. The altitude at Chuka Forest Station is 1700 m. Chuka experiences the same pattern of bimodal rainfall as Muguga, but receives a higher rainfall averaging 1500 mm per year. There are two dry months at the beginning of the year and four others from June to early October. Detailed meteorological data are not available at Chuka. At Embu (00° 30'S, 37° 27'E) which is about 20 km to the south-west of Chuka and at an altitude of 1500 m a.s.l., the mean annual temperature is 18.7 °C (Kenya Meteorological Department, 1984).

The daily maximum and minimum temperatures are 24.0 °C and 13.4 °C respectively. Because Chuka is about 200m higher than Embu, the mean annual temperature should be lower by about 1.2 °C. The relative humidity at Embu is 70% and is probably slightly higher at Chuka. The mean daily solar radiation is 433 cal. cm^{-2} and monthly distribution is shown in Figure 2.1. The solar radiation at Chuka is probably close to that of Embu, but lower than that at Muguga because of increased cloud cover near the mountain.

The soils at Chuka Forest are deep, well drained volcanics. They are dark reddish to dark brown strong acidic loams.

In the eastern and southern slopes of Mt. Kenya where annual rainfall is between 1250 and 2250 mm, the natural forests have been referred to as temperate rain forests (Battiscombe, 1936) and broad-leaved moist and intermediate forests (Trapnell and Langdale-Brown, 1962; Brown and Cocheme, 1969). In general these forests appear to be intermediate between the tropical rain forests and the tropical montane forests. The dominant species are *Ocotea usambarensis* (East African Camphor) and *Podocarpus milanjianus.* These forests are also known as camphor forests (Battiscombe, 1936). Other species associated with these two main species are *Strombosia scheffleri, Casearia battiscombei, Syzigium guineense, Prunus africana, Olea capensis, Croton macrostachyus, Macaranga kilimandscharica, Neoboutonia macrocalyx, Newtonia buchananii, Fagara macrophylla*, etc. *Cordia africana* and *Vitex keniensis*, which are the major study species, also occur in these forests. Although commercial exploitation of natural forests in Chuka has not been severe, *Cordia africana* seems to have been overcut for use in making bee-hives. A small area of Chuka Forest has been converted to tree plantations of *Vitex keniensis* and eucalypts. Outside the forest reserve, *C. africana* is scattered in farmlands as an agroforestry species.

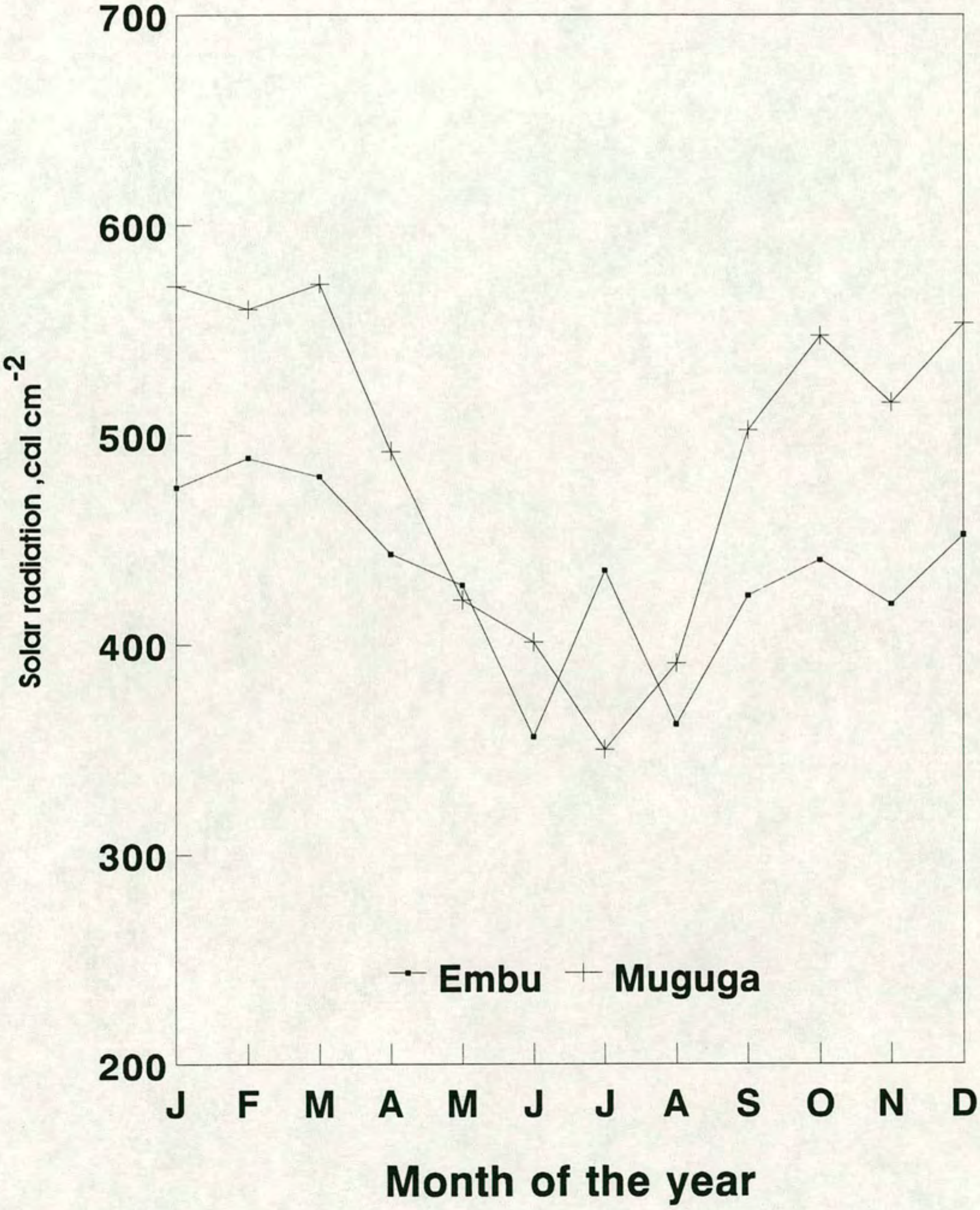

Figure 2.1. Monthly distribution of solar radiation at Muguga and Embu. Embu is 20 km south-west of Chuka Forest Station.

2.2 STUDY SPECIES

2.2.1 *Cordia africana* Lam. (Boraginaceae)

Until more recently, this species was called *Cordia abyssinica* R. Br. It is a deciduous tree generally 10 m in height, but occasionally growing up to 25 m (Dale and Greenway, 1961). Mature trees of *C. africana* may attain a diameter at breast height of 100 cm, but probably only on fertile sites in high rainfall areas. *C. africana* is a highly forked tree that flowers early in its life. The fruit is a drupe with 1 - 3 small seeds in a stony shell. It displays seed dormancy (Ahenda, 1991).

C. africana seems to have a wide geographical range in moist and savanna areas of tropical Africa. It is a tree found in the savanna and forest edge in Uganda (Eggeling and Dale, 1961). In Ethiopia, *C. africana* is widely distributed both in forest edges and inside mixed forests where it attains height of up to 30 m (Mihretu, 1994). This species also occurs in cultivated areas of Ethiopia as a forest remnant (Bekele *et al,* 1993). In the Sudan, it is found in high rainfall savannas and water courses at elevation of up to 1350 m a.s.l. (Sahni, 1968; Amin, 1990). *C. africana* is common near villages in Ghana and is often planted (Irvine, 1961).

In Kenya, *C. africana* has a wide distribution, although it occurs mainly in high rainfall areas between about 1200 and 2000 m a.s.l. It is found both in forest areas and in the farmlands. However, it seems to be localised in the forest probably because of overcutting. Regeneration of *C. africana* in closed natural forests seems to be rare, but it has been observed to regenerate well in partially exploited forests of Kakamega in Western Kenya. This seems to suggest that seedlings of *C. africana* are light demanding. The species grows on a wide range of soils from light sands to heavy clays. It produces a light, valuable timber which is now scarce in Kenya (Bengough, 1970). It has become an important agroforestry species, being used as a shade tree for agricultural crops. Because of its deciduous nature, its large leaves produce a good mulch which enhances soil conservation and fertility. The species is also important as an amenity tree. Due to its many uses, the cultivation of *C. africana* in Kenya is on the increase. However, little is known about its ecological adaptation, especially its light requirements.

2.2.2 *Vitex keniensis* Turill (Verbenaceae)

This species is commonly called meru oak in Kenya. It is a deciduous tree growing to a height of up to 40 m. The tree flowers annually from the age of 5 - 6 years. The fruit is a drupe with 3 - 4 seeds. *V. keniensis* has a restricted natural range. It occurs in forests of north-east and eastern slopes of Mt. Kenya, in areas with annual rainfall of 1500 - 2250 mm and at an elevation of 1500 - 1800 m a.s.l. It prefers deep well drained soils. *V. keniensis* does not seem to occur in other parts of Africa, although a related species, *Vitex fischeri* Gurk is found is Zimbabwe (White, 1962).

In natural forests, *V. keniensis* seems to regenerate in canopy gaps. Its seedlings usually germinate under the parent tree in forest edges. However, seedlings do not survive under dense shade. Foresters in Kenya generally consider *V. keniensis* as a light demanding species (Kenya Forestry Dept, 1969).

V. keniensis is a moderately fast growing species (Kigomo, 1981). It is one of the most important valuable timber trees in the country and is a major indigenous hardwood in plantation programmes. It is grown on a rotation of about 40 years. It is also used in enrichment planting in forest areas with poor stocking of commercial timber species. The tree has also gained popularity as an ornamental tree and its planting has increased outside its ecological range.

2.2.3 *Olea capensis* L. (Oleaceae)

Until recently this species was called *Olea welwitschii* (Knobl. Gilg & Schellebn). It is commonly called elgon olive or elgon teak. *O. capensis* is generally an evergreen forest tree with a small crown and a long straight bole (Teel, 1984). It grows up to a height of 30 m (Dale and Greenway, 1961). It is widely distributed in Kenya, Uganda and Ethiopia (Dale and Greenway, 1961; Bekele *et al,* 1993), but has a restricted range in Northern Tanzania (Parry, 1957). The species occurs between 1300 and 2000 m a.s.l. and in moist forests receiving annual rainfall of 1200 - 2000 mm. It prefers deep well drained soils.

The ecological status of *O. capensis* is not clear as some observations indicate that it is a pioneer species, while others suggest that it is shade tolerant. Eggeling (1947) found it among the species in colonising forests and grasslands on the edge of Budongo forest in Uganda.

Seedlings of this species which germinate in large numbers below the parent tree in closed forests do not seem to survive for more than a few years or to grow to sapling stage. However, in Chuka Forest, *O. capensis* regenerates and grows to sapling stage under low irradiance in plantations of *V. keniensis*. Parry (1957) reported *O. capensis* as being liable to sun scorch, although its seedlings could still be planted successfully under full sunlight.

O. capensis produces one of the most beautiful timbers in East Africa for decorative work (Parry, 1957). Because the species has been over-exploited and its timber is becoming scarce, it has become an important species in restocking degraded forests in Western Kenya.

2.2.4 *Markhamia lutea* (Benth.) K. Schum (Bignoniaceae)

This species is commonly called siala in Western Kenya. It is an evergreen slender-boled tree 10 - 15 m tall but occasionally attaining a height of 24 m (Dale and Greenway, 1961). The tree produces long and thin capsular fruits containing light winged seed.

M. lutea appears to be widely distributed in tropical Africa. It is widespread in Kenya occurring in moist areas between 1300 and 1800 m a.s.l, but commonly around Lake Victoria. In its natural habitat, it has been reported occurring at forest edge and riverine areas in Kenya and Uganda (Dale and Greenway, 1961; Eggeling and Dale, 1961) and in savanna areas in Ghana (Irvine, 1961). The species is widely distributed in Ethiopia in forest edges and river valleys up to 2000 m a.s.l (Bekele *et al*, 1993).

It prefers well drained loams but also tolerates heavy clays. *M. lutea* was one of the first indigenous species to be cultivated in Uganda in the early 1920`s (Kriek, 1968). The species is widely planted in farmlands in Western Kenya. It is moderately fast growing and is usually regenerated by coppicing. It is mainly used for production of building poles and is also a popular amenity tree with bright yellow flowers.

2.3 GENERAL METHODS

2.3.1 Materials

Plants of *C. africana, V. keniensis* and *M. lutea* were raised from seed, while those of *O. capensis* were from wildings. The seeds of each species were a mixture of lots collected from about 30 mother trees from the same area. They were stored at 3.0 °C at the Kenya Forestry Seed Centre (KFSC). Seeds of *C. africana* and *V. keniensis* were soaked in cold water for 48 hours before sowing to improve the speed of germination. The forest soil used in growing the experimental seedlings was collected from the top 15 cm layer at Kerita Forest, 25 km north of Muguga. Samples of this soil were analysed for physical and chemical properties and the results showed that it was sandy clay loam with pH of 6.9 and total nitrogen concentration of 0.78%. The other nutrients were at moderate levels (P, 1.3 ppm; K, 50 ppm). The micro-elements were in the following amounts in parts per million (ppm): Zn, 12.0; Cu, 5.0; Fe, 760.0 and Mn, 640.

In all nursery experiments the seedlings were generally watered daily in the morning and evening. The plants were regularly sprayed with insecticide to protect them from defoliation by *Systates surdis* Mysh. (Curculionidae). This beetle was common in the nursery, but spraying proved quite effective.

2.3.2 Measurements of Light, Temperature and Humidity

Measurements of photosynthetic photon flux density (PPFD), temperature and humidity were made continuously with sensors connected to a battery-powered datalogger (Deltalogger, Delta-T Devices, Cambridge, U.K.). The PPFD was measured by use of inexpensive PAR quantum sensors made at the Department of Forestry and Natural Resources, University of Edinburgh. These sensors were calibrated against a standard sensor (Li-1900 SB, Li-Cor Inc. Lincoln, NB, USA). In all experiments, the logger was programmed to collect PPFD data from each quantum sensor every 30 seconds and to compute hourly averages before storage in the RAM. The mean and daily PPFD were calculated in all experiments and also expressed as percentage of the full sunlight.

The temperature and relative humidity (and saturation vapour pressure deficit, VPD) were measured with fine soldered copper constantan thermocouples (B10 B51843

Type T, T.C. Ltd. Uxbridge, U.K.). The psychrometric unit, which was unventilated, consisted of thermocouples to measure the wet and the dry bulbs temperatures. The units were shielded from direct radiation with U-shaped white-painted plastic cups about 3 cm in diameter and 9 cm in length. The wet bulb sensor had a cotton wick at the end dipped in a 50 mm plastic bottle containing distilled water. The water levels in the bottles were maintained at the same level near the top by regular addition of water. The logger recorded the temperatures from the sensors every 5 minutes and computed the hourly average.

2.3.3 Data Collection

Destructive harvests were made in all the nursery experiments. The shoot of each seedling was separated from the roots at the root collar. Plant height was measured from the root collar to the terminal bud of the main stem. The number of leaves present and those abscised were counted. The shoot was then separated into leaves and stem. The stem included the petioles. The leaf areas of each seedling were measured using an automatic leaf area meter (Model AA7, Hayashi Denko Co. Ltd., Japan). The roots were washed free of the soil in 1.0 mm sieves. The leaves, stem and roots were oven dried at 70^0C for 48 hours for dry weight determination. Weighing (to constant weight) was done separately for each plant part. Any soil particles and gravel locked in between the roots were removed before the determination of the root dry weight. No allowance was made for either leaf areas or dry weights of the abscised leaves.

The net assimilation rate (NAR) is the rate of increase in plant dry weight per unit of leaf area per unit of time. It was calculated using the following equation from Hunt (1978):

$$NAR = \frac{W_2 - W_1}{t_2 - t_1} \cdot \frac{\ln A_2 - \ln A_1}{A_2 - A_1}.$$

Where W_1 and W_2 are the plant dry weights and A_1 and A_2 are mean plant leaf areas in the first harvest (t_1) and second harvest (t_2) respectively. This equation is only valid when the plant dry weight and leaf area are linearly related (Hunt, 1978), as determined in this case by linear regression.

2.3.4 Data Analysis

For the nursery experiments, mean values were determined for total dry weight, height, leaf area and numbers of leaves present and abscinded. The following were derived from the data on dry weights and leaf areas: leaf area ratio (LAR) as leaf area per unit of total seedling dry weight, cm^2g^{-1}; leaf weight ratio (LWR) as leaf dry weight per unit of total seedling dry weight, gg^{-1}; stem weight ratio (SWR) as stem dry weight per unit of total seedling dry weight, gg^{-1}; root weight ratio (RWR) as root dry weight per unit of total seedling dry weight, gg^{-1}; specific leaf area (SLA) as leaf area per unit of leaf dry weight, cm^2g^{-1}; and shoot:root ratio (SRR) as shoot dry weight per unit of root dry weight, gg^{-1}.

The relative growth rate (RGR) is the rate of increase in plant dry weight per unit of dry weight per unit of time. It was calculated using the following equation by Hunt (1978):

$$RGR = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}.$$

Where W_1 and W_2 are mean plant dry weights during first harvest (t_1) and the second harvest (t_2) respectively. Analysis of Variance (ANOVA) was carried out for each of the parameters to determine significant difference between means.

CHAPTER 3

GROWTH RESPONSES OF NURSERY GROWN SEEDLINGS TO IRRADIANCE AND NUTRIENT SUPPLY

3.1 INTRODUCTION

Since the early 1980s, many studies have been undertaken on the responses of seedlings of tropical trees to various levels of irradiance or canopy gaps of various sizes (Sasaki and Mori, 1981; Fetcher *et al*, 1983; Whitmore and Bowen, 1983; Oberbauer and Strain, 1985; Kwesiga, 1985; Bongers *et al*, 1988; Thompson *et al*, 1988; Kamaluddin, 1991). The results of these studies generally show that seedlings of tropical trees respond to irradiance according to the two ecological groups of pioneer and shade-tolerant species. Pioneer species have been associated with canopy gaps (Whitmore, 1985 and 1989; Popma and Bongers, 1988; Oldeman and Dijk, 1991). They show rapid rise in relative growth rate with increasing levels of light (Fetcher *et al*, 1983; King, 1991) and are likely to grow better in open areas or large gaps. In contrast, shade-tolerant species survive and maintain active growth under deep shade (Kwesiga, 1985; Popma and Bongers, 1988). Such species are important in natural regeneration or enrichment planting in least disturbed forest areas.

While the tropical trees have been classified as either pioneers or shade tolerant, some species do not seem to fall strictly into either group. Some are known to show complex responses to light resembling both the pioneers and shade-tolerant species in different aspects of their responses (Popma and Bongers, 1988).

Canopy gaps are areas of increased resources, both light and nutrients (Kamaluddin, 1991). However, seedlings of some tree species do not withstand exposure to increased irradiance and grow better with some degree of shading (Nicholson, 1960; Ampofo and Lawson, 1972; Sasaki and Mori, 1981; Whitmore, 1985; Kigomo, 1989; Turner and Newton, 1990).

Although the role of light in regeneration of tropical trees has received the most attention, the supply of nutrients is also important (Kamaluddin, 1991) and has major interaction with the light environment. For example, the supply of nutrients to seedlings, particularly at higher levels, may change the photosynthetic capacity of the leaf (Thompson *et al*, 1988; Riddoch *et al,* 1991). As forest disturbance caused by logging, clearing and burning do result in substantial losses of nutrients (Jordan, 1991), this is likely to hinder the growth and establishment of seedlings. However, disturbance may also be accompanied by a flush of nutrients as a result of decomposition of foliage from felled trees. Such an increase in nutrient supply in some of the impoverished tropical soils may be of as much significance as the photon flux density (Riddoch *et al*, 1991). Mycorrhizas are also important in establishment and growth of seedlings especially in nutrient poor soils (Herrera *et al*, 1991; Janos,1983 and Jordan, 1991).

In Kenya, attempts are being made to improve the management of the remaining natural forests and to increase the forest/tree cover. To achieve these objectives, forestry programmes include: protection of natural forest to improve natural regeneration; enrichment planting in areas depleted of valuable species; rehabilitation of degraded forest areas and promotion of agroforestry. The use of indigenous species in these programmes is being encouraged. However, appropriate species for each silvicultural system or programme have not been identified. Where planting is being done, the selection of species is based on inadequate local experience. As a result some species have tended to be planted in areas with very different light climates with varying level of success. This is because there is inadequate information on their requirements for light. An understanding of the responses of individual species to different levels of irradiance is therefore necessary for any successful regeneration programmes.

With the exception of the studies by Synnott (1975) and Kigomo (1989) no other investigations seem to have been done in East Africa on responses of seedlings of tropical trees to different levels of light. The investigations by these two workers did not also adequately address the role of light and shade in forest regeneration. The aim of the present experiment was therefore to explore the role of light and nutrient supply on growth of seedlings of two important indigenous trees in Kenya. The species are *C. africana* and *V. keniensis*. These species are considered as light demanders but seem to grow well both inside and outside forest areas and in soils of varying nutritional status. The hypothesis is that the two species grow faster under some degree of shading especially in nutrient-rich soils. The study attempts to answer the following questions: Can *C. africana* and *V. keniensis* maintain positive growth in shade? Is their growth adversely affected under full sunlight? Is their growth in the shade and the full sunlight affected by the supply of nutrients? How do the two species adapt to varying levels of irradiance? Is it appropriate to use the two species in the present silvicultural systems in Kenya? In particular, which regeneration systems are most appropriate? Natural regeneration in closed forest canopies; enrichment planting in small, medium or large gaps; growing in open areas for establishment of plantations or/and under agroforestry systems?

In this nursery experiment, seedlings of the two species were grown under four levels of irradiance and two nutrient regimes in semi-controlled nursery conditions. Three types of artificial shade were used to simulate light environment in forest gaps. Their effects on growth of seedlings were compared to seedlings exposed to full sunlight. Although light quality under artificial shade differs from forest shadelight, this was not investigated in the present experiment. However, the three types of shade cloth used were near neutral in spectral transmission, hence the experiment investigates the effects of irradiance without the confounding effects of changes in light quality, that occur in nature.

3.2 MATERIALS AND METHODS

3.2.1 Experimental Area

This experiment was conducted at Muguga site whose details were described earlier in Chapter 2.

3.2.2 Treatments and Experimental Design

This was a factorial (split-split plot) experiment: 4 light treatments (19, 44, 52 and 100% of full sunlight) x 2 species (*C. africana* and *V. keniensis*) x 2 nutrient (low and high). A randomised block design with three replications was used. Randomisation of the treatments was carried out as follows: light treatments within the blocks; species within the light treatments and nutrient levels within the species. There were 42 seedlings in each sub-sub-plot.

3.2.3 Potting Soil and Nutrient Levels

The potting soil for the low nutrient treatment had three ingredients: forest top soil, 6.4 mm building gravel and "mycorrhizal" soils. The latter were from the rooting zones of naturally growing *C. africana* and *V. keniensis* (collected from Nairobi University Farm in Kabete and Chuka Forest Reserve respectively). They were included in the potting mixture because preliminary tests indicated the presence of mycorrhizas (Vesicular-arbuscular mycorrhizas, VAM) in the roots of *C. africana* and *V. keniensis*. The "mycorrhizal" soils were premixed in equal parts before mixing with the other two ingredients. The three ingredients were mixed in a concrete mixer in the ratio of 5:1:1 by volume of forest soil, gravel and "mycorrhizal" soils respectively.

The potting soil for the high nutrient treatment comprised of forest top soil, 6.4 mm gravel, "mycorrhizal" soils and cow manure made in the ratio of 5:1:1:1 by volume respectively. For every 8 litres of these ingredients 12.0 g of NPK fertiliser was added. The ingredients were also mixed in a concrete mixer. The NPK fertiliser was a compound with 20%N, 10%P_20_5 and 10% K_20. The rate of application was 2.46 g per pot supplying nutrients per seedling as follows: N, 0.049 g; P, 0.11 g and K, 0.20 g. The cow manure was collected in January 1992 and kept in the nursery for six months before use. The exact nutrient status of this mixture was not determined. No additional nutrients were provided during the experiment.

3.2.4 Plant Materials

Seeds of *C. africana* (KFSC Batch No. 139029/91) were collected in November 1991 from Aldai and Shinyalu Divisions in Western Kenya. These areas lie at the elevation of between 1600 and 2000 m a.s.l. Seeds of *V. keniensis* (KFSC Batch No. 431045/91) were also collected about the same time from Ragati Forest Reserve on the southern slopes of Mt. Kenya. Ragati Forest is about 2100 m a.s.l.

On 15th June 1992, the seeds of both species were sown into 9.5 cm diameter black polythene pots each with capacity of 1.64 litres. The pots were perforated at the base to improve drainage. Three seeds were sown per pot at the depth of about 2.0 cm. Sowing was completed the same day. Surplus seeds from the same samples were also sown on the same day in seedbeds containing equal parts of forest soil and river sand. The pots and the seedbeds were not shaded because the weather was cloudy and cold with daily maximum and minimum temperatures of 18.6 and 5.4 °C respectively. Seeds of these species usually germinate faster under unshaded conditions in the nursery.

Germination commenced two weeks after the date of sowing. The germination in seedbeds was high but staggered in pots. In order to obtain uniform seedlings, transplanting into blank pots was carried out on 13th July, 1992. Although the seedlings used in transplanting were mainly from the seedbeds, some were also from the pots with more than two seedlings. The transplanting of seedlings among the pots was only done within the same nutrient regime. The cotyledons of most seedlings were fully expanded at the time of transplanting.

The seedlings were allowed to establish for about five weeks from 14th July to 16th August 1992. During this period dead seedlings were replaced. On 10th August 1992, the seedlings were singled in pots that had two or more. By this time about 20% of the seedlings of *V. keniensis* showed leaf chlorosis. The seedlings grown in low nutrient regime were mainly affected and this seemed to be due to nitrogen deficiency. About two weeks after transplanting, the cotyledons in seedlings of *C. africana* were scorched. Seedlings grown in both nutrient regimes were affected. The scorching also later affected the first to the third leaves. Some of the affected leaves died gradually while others persisted but with necrotic spots. However, none of the seedlings died as a result of scorching.

About five weeks after transplanting, on 17th August 1992 the seedlings were randomly allocated to irradiance treatments. Each pot was then labelled with white paint. At the start of the experiment the seedlings of *C. africana* averaged 2.1cm in height. The first two leaves were fully expanded but on the average, one of the cotyledons had been shed in each seedling. The seedlings raised in the high nutrient regime were growing more vigorously than those raised in the low nutrient regime. At this time, seedlings of *V. keniensis* averaged 2.8 cm in height. The first pair of true leaves was fully expanded and none of the cotyledons had abscised. Some of the seedlings grown in the low nutrient regime continued to show leaf chlorosis, while those in high nutrient did not. The seedlings were regularly moved around to reduce the effects of location within the sub-subplot.

3.2.5 Light Treatments and Microclimate

The four light treatments were three levels of shade (19, 44 and 52% of full sunlight) and full sunlight. The shade levels were obtained by use of shade-cloth (plastic netting) of different light interceptions. The choice of shade levels was mainly determined by local availability of the shade-cloth in Kenya.. Each frame was 2.0 x 1.0 x 1.0 m in length, width and height respectively. The shade-cloth covered the top and extended 75 cm down on all sides. A ventilation gap of 25 cm was left at the bottom.

Microclimatic data on photosynthetic photon flux density (PPFD), temperature and humidity were collected for 16 days from 15th to 30th September 1992. The procedures used are described in Section 2.3.2. Illumination inside the shade houses was also measured once a week (between 12.00 and 13.00 hours local time) for six weeks. Measurements were made with two hand-held illuminance meters (Minolta T-1, Minolta Co. Ltd. Japan).

The irradiance levels received inside the shade houses as a percentage of that in the full sunlight were: 19% for dense shade (low irradiance); 44% and 52% for the two levels of moderate shade (medium irradiance). The relative light illuminance (RLI) as percentage of that outside the shade houses were: dense shade (20%) and moderate shades (44% and 52%). The percent level of PPFD and that of RLI were therefore similar.

Figure 3.1 shows the diurnal variations of average PPFD within the four light treatments during a period of 16 days in September 1992. The mean daily PPFD (μ mol m^{-2} s^{-1}) was: dense shade (182.4), moderate shades (424.3 and 495.8) and full sunlight (958.8). The mean total daily PPFD (mol m^{-2} d^{-1}) was: dense shade (7.9), moderate shades (18.3 and 21.4) and full sunlight (41.4). The peaks in all the light treatments occurred at about noon local time. The quality of light (measured after the end of the experiment) transmitted by the three types of shade-cloth had red/far-red ratio of 1.05 compared to that of 1.07 in the full sunlight. The shading materials were therefore near neutral in their spectral transmission and did not simulate forest shade light, but provided appropriate environments for the determination of the effects of irradiance without the confounding effects of changed light quality.

1981; Chazdon and Fetcher, 1984b; Longman and Jeník, 1987). The irradiance level of 19% of full sunlight in the dense shade of this experiment was therefore considerably higher than that in the understorey of tropical forests, but close to that recorded in a light or medium gap of 400 m^2 (Fetcher *et al*, 1983; Chazdon and Fetcher, 1984 a & b).

In the moderately shaded treatments, the total daily PPFD of between 18.3 and 21.4 mol m^{-2} d^{-1} were within the range of 13.7 and 33.9 mol m^{-2} d^{-1} recorded in a forest clearing of 5000 m^2 (Chazdon and Fetcher 1984 a & b). The irradiance in the moderately shaded treatments of this experiment therefore seem to have adequately simulated the irradiance in large forest gaps or clearings. The total daily PPFD of 41.4 mol m^{-2} d^{-1} in the full sun was slightly lower than that of 44.2 mol m^{-2} d^{-1} measured by Björkman and Ludlow (1972) in an open site outside a sub-tropical rain forest in Queensland, Australia. However, it was between the range of 35.3 and 46.8 mol m^{-2} d^{-1} recorded by Lee (1989) in an area outside a moist deciduous tropical forest in India. The irradiance under the full sun in this experiment seem to have been typical of that in exposed areas outside tropical forests.

Figure 3.1 shows the diurnal variation in mean temperature within the light treatments as measured by use of the datalogger at Muguga. The mean air temperatures were: 15 °C in the dense shade; 15.9 °C under moderate shade levels and 16.5 °C in the full sun. The minimum and maximum temperatures occurred at 06.00 and 15.00 hours local time. The mean minimum daily temperature was about 10 °C in all the irradiance treatments while the maximum ranged from 21.9 °C in the dense shade to 24.8 °C under the full sun. Although the mean temperature in the dense shade was lower than in other treatments, the differences were small (less than 1.0 °C). The temperature conditions within the treatments were therefore generally similar and were unlikely to contribute to any differences in growth of seedlings. The mean air temperature at the experimental site was about 10 °C lower than in lowland tropical forests. This was due to high elevation of about 2000 m a.s.l. on the experimental site. The low temperatures are, however, typical of those experienced in tropical montane forests in the highlands of East Africa.

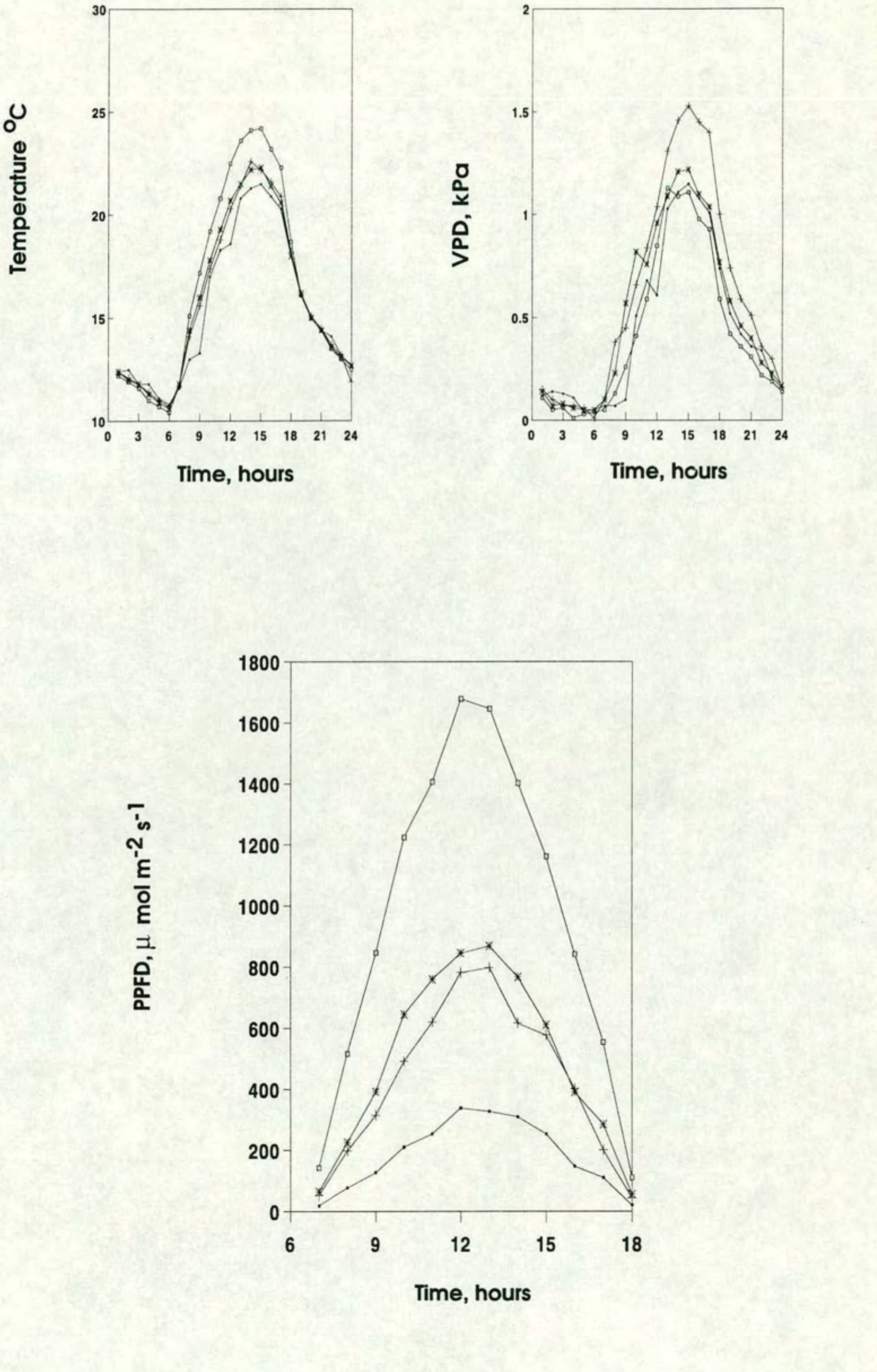

Figure 3.1. Mean daily PPFD, mean temperature and VPD received within the light treatments.

Figure 3.1 shows the variation in the vapour pressure deficits (VPD) within the light treatments. The mean VPD (kPa) in the four light treatments were: dense shade (0.45); moderate shades (0.61 and 0.52) and full sunlight (0.42). The latter was expected to be the highest, but seems to have been affected by some errors in the wet-bulb sensor. The errors were probably caused by water contamination in the container or poor soldering of the thermocouple wires. In all the treatments, the maximum and minimum VPD occurred about 15.00 and 05.00 hours local time respectively.

3.2.6 Data Collection and Analysis

Two destructive harvests were made at the age of 37 and 65 days after the start of the experiment. In each sub-subplot, 10 seedlings were sampled randomly at each harvest. This left a total of 22 seedlings out of 42 in each sub-subplot for the next experiment (Chapter 4). The procedures followed during harvesting and analysis are described in Sections 2.3.3 and 2.3.4 respectively.

3.3 RESULTS

The means of the various variables assessed are given in Tables 3.1 and 3.2. The summary and detail of results on analysis of variance are also shown in Table 3.3 and Appendix I respectively.

3.3.1 Dry Weight Production

The mean total dry weight (including roots stem and leaves) of seedlings of *C. africana* and *V. keniensis* was significantly affected by the light and nutrient treatments at the final harvest (Table 3.3). The two species also differed significantly. Seedlings of *C. africana* produced three times greater dry weight than those of *V. keniensis*. All the interactions were also significant. As shown in Figure 3.2, the dry weight production generally increased with increasing irradiance, except for seedlings of *V. keniensis* grown in the low nutrient regime.

Table 3.1: Mean ± Standard errors of some characteristics of seedlings of *C. africana* and *V. keniensis* grown under different levels of irradiance and two nutrient regimes.

Light Treatment (% full sunlight)	Species	Nutrient level	Size Parameter					
			Total dry weight, g	Height, cm	Leaf area per plant, cm^2	Number of leaves present	RGR $g\ g^{-1}\ wk^{-1}$	NAR, $g\ m^{-2}\ wk^{-1}$
19	*C. africana*	Low	0.66±.06	5.9±0.41	112.7±10.5	7.4±0.3	0.29±07	19.57±4.52
		High	1.36±0.06	8.4±0.46	236.2±15.8	7.9±0.1	0.33±0.03	19.39±41.49
	V. keniensis	Low	0.36±0.49	6.9±0.04	49.9±9.7	9.1±0.5	0.20±0.03	14.70±2.97
		High	0.48±.07	8.3±0.64	82.5±14.0	0.3±0.2	0.26±0.03	15.90±2.28
44	*C. africana*	Low	1.04±.24	7.6±1.09	169.1±30.6	8.0±0.3	0.34±0.00	24.73±3.26
		High	2.75±.50	11.2±1.33	375.4±63.3	10.8±0.6	0.40±0.03	30.83±3.00
	V. keniensis	Low	0.47±.02	7.4±0.16	51.3±4.3	10.0±0.9	0.22±0.02	20.97±2.50
		High	0.76±.08	8.3±0.31	95.6±9.9	11.2±0.8	0.32±0.01	25.61±1.94
52	*C. africana*	Low	1.28±.21	8.1±0.35	170±17.9	9.3±0.5	0.36±0.01	31.30±1.52
		High	3.18±.69	10.8±1.02	371.6±59.9	10.3±0.7	0.40±0.02	32.95±3.71
	V. keniensis	Low	0.48±0.04	7.6±0.15	53.9±06.4	10.8±0.7	0.26±.04	25.10±3.79
		High	0.84±.08	8.8±0.45	109.3±12.2	11.0±1.1	0.32±0.01	25.18±1.12
100	*C. africana*	Low	1.97±.24	8.3±0.17	208.3±14.8	10.6±0.4	0.44±0.02	46.50±2.70
		High	3.20±.26	9.6±0.60	333.9±36.9	9.4±1.2	0.32±0.01	32.84±0.64
	V. keniensis	Low	0.48±.06	7.4±0.04	41.7±4.9	11.9±0.4	0.24±0.05	29.46±2.75
		High	1.10±.15	9.3±0.64	108.9±13.6	13.5±0.3	0.36±0.03	37.86±3.66

Table 3.2: Mean ± Standard errors of some characteristics of seedlings of *C. africana* and *V. keniensis* grown under different levels of irradiance and two nutrient regimes.

Light Treatment (% full sunlight)	Species	Nutrient level	Size Parameter				
			LAR, $cm^2\ g^{-1}$	SLA, $cm\ g^{-1}$	LWR, $g\ g^{-1}$	SWR, $g\ g^{-1}$	RWR, $g\ g^{-1}$
19	*C. africana*	Low	172.0±1.0	284.6±15.6	0.61±0.03	0.15±0.01	0.25±0.04
		High	173.2±4.2	267.0±2.5	0.65±0.02	0.16±0.01	0.19±0.02
	V. keniensis	Low	152.4±13.3	276.9±11.5	0.55±0.03	0.18±0.01	0.27±0.02
		High	172.9±9.2	285.0±3.8	0.61±0.03	0.17±0.00	0.22±0.03
44	*C. africana*	Low	164.6±12.8	275.3±13.4	0.60±0.02	0.15±0.01	0.26±0.03
		High	136.6±2.1	211.7±0.9	0.64±0.01	0.16±0.01	0.20±0.02
	V. keniensis	Low	109.61±4.1	205.9±16.7	0.54±0.04	0.17±0.01	0.29±0.04
		High	125.3±0.6	209.1±8.3	0.60±.02	0.16±0.00	0.24±0.03
52	*C. africana*	Low	134.2±9.6	226.8±23.3	0.59±.02	0.15±0.00	0.26±0.02
		High	118.2±7.8	191.4±2.5	0.62±0.03	0.14±0.00	0.24±0.04
	V. keniensis	Low	112.1±4.8	206.8±2.7	0.54±0.02	0.17±0.01	0.29±0.01
		High	130.2±2.9	212.8±6.4	0.61±0.01	0.16±0.01	0.22±0.02
100	*C. africana*	Low	106.4±6.2	179.17±9.9	0.59±0.01	0.14±0.01	0.27±0.01
		High	104.3±6.6	164.8±6.3	0.063±0.02	0.15±0.01	0.22±0.02
	V. keniensis	Low	86.1±5.4	167.9±4.3	0.51±0.02	0.17±0.00	0.32±0.02
		High	991.1±7.1	172.4±12.0	0.57±0.00	0.17±0.01	0.25±0.01

Table 3.3: The effect of light and nutrient treatments on growth, size parameters, morphology and dry weight distribution on seedlings of *C. africana* and *V. keniensis*.

Variate	Treatments and Interactions						
	Light L	Species S	Nutrients N	L x S	L x N	S x N	L x S x N
Total Dry Weight	***	****	****	*	*	***	*
Height	***	*	****	ns	ns	**	*
RGR	*	***	***	ns	*	***	**
NAR	***	***	ns	ns	ns	*	**
LAR	****	**	ns	ns	**	****	*
LWR	ns	****	****	ns	ns	ns	ns
SWR	ns	****	ns	ns	ns	ns	ns
RWR	ns	****	****	ns	ns	ns	ns
SRR	ns	***	****	ns	ns	ns	ns
SLA	****	ns	***	**	*	****	*
Leaf area/seedling	**	****	****	**	ns	****	ns
No. of leaves present in the second harvest	****	****	*	ns	ns	ns	ns
No. of leaves shed by the second harvest	**	****	****	**	**	****	***

Symbols: ns = not significant at $P < 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = 0.001; **** = 0.0001

For details see also Appendix I.

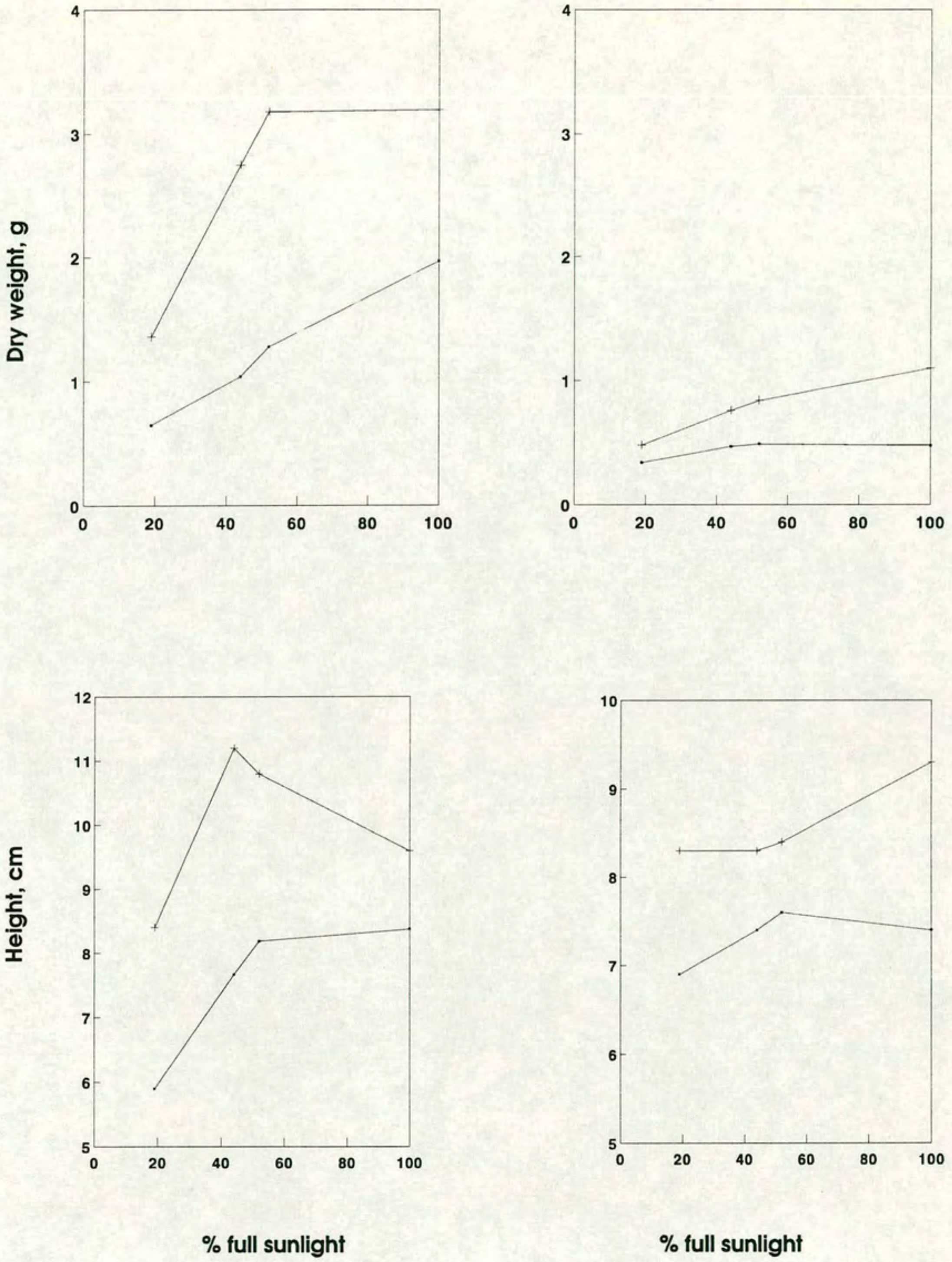

Figure 3.2. Means of total dry weight and height of seedlings of *C.africana* (left) and *V.keniensis* (right) grown under low (---•---) and high (----+---) nutrient regimes and different irradiance levels.

Seedlings grown under the dense shade had significantly lower dry weight than those raised under the two levels of moderate shade and the full sunlight treatments. The dry weight of seedlings grown in both levels of moderate shade did not differ significantly from those grown in the full sunlight.

Seedlings grown under high nutrient regime had significantly greater dry weight than those raised in the low nutrient regime. In *C. africana,* seedlings grown under low nutrient regime responded positively to increase in irradiance while the dry weight of those grown under the high nutrient regime levelled off at moderate shade level of 52% of full sun.

3.3.2 Height Growth

Figure 3.2 shows the height growth of seedlings grown under the different levels of irradiance and nutrient treatments. The irradiance treatments significantly affected the height growth of seedlings (Table 3.3). Seedlings grown in the dense shade had significantly lower height than those grown under moderate shades and in the full sun. Seedlings of *C. africana* were significantly taller than those of *V. keniensis*.

Seedlings grown under high nutrient regime had higher growth in height than those grown in the low nutrient regime. Seedlings of *C. africana* grown in both nutrient regimes and those of *V. keniensis* grown in low nutrient regime had maximal height growth under irradiance levels of 44 and 52% of full sunlight. Height of seedlings of *V. keniensis* raised in high nutrient regime was highest under full sunlight. These differences resulted in significant interactions between the species and nutrient treatments and among the three factors.

3.3.3 Growth Analysis

The effects of irradiance and nutrient treatments on relative growth rate (RGR) of seedlings of *C. africana* and *V. keniensis* are shown in Figure 3.4. Table 3.3 also gives a summary of results using analysis of variance. RGR was significantly affected by the levels of irradiance and nutrient treatments. It was lowest under the dense shade and generally increased with increasing irradiance. However, there were no significant differences between the RGR of seedlings grown under the two moderate shade treatments (44 and 52% of full sunlight) and full sunlight. Seedlings of *C. africana* had higher RGR than those of *V. keniensis.*

The seedlings grown under the high nutrient regime had significantly higher RGR than those grown in low nutrient regime. In both species, the supply of nutrients at high level enhanced the RGR under moderate shade with irradiance levels of 44 and 52 % of full sunlight (Figure 3.4). The combination of high irradiance and high nutrients enhanced the RGR of seedlings of *V. keniensis,* but depressed that of *C. africana*. On the other hand, the combination of high irradiance and low nutrient enhanced the RGR of seedlings of *C. africana* but slightly depressed that of *V. keniensis*. The interaction between light treatments and species was not significant, but all other interactions were. The significant interactions were mainly due to the different responses of the two species to nutrient supply when grown under full sunlight.

The irradiance treatments significantly affected the NAR but the nutrient treatments did not (Table 3.3). As shown in Figure 3.4, values of the NAR were lowest for seedlings grown in the dense shade (19% of full sunlight) and highest for those grown under the full sunlight conditions. Seedlings of *C. africana* had significantly higher NAR than those of *V. keniensis*. However, the two species displayed similar trends in their responses. Among the four interactions of species x nutrient, seedlings of *C. africana* grown under high nutrient had maximum NAR under moderate shade levels (44 and 52 % of full sunlight). The values of the NAR of the rest of the interactions were highest under full sunlight. Interactions between the species and nutrient treatments and the three-way interactions (light x species x nutrient) were significant.

3.3.4 Leaf Morphology and Biomass Distribution

The leaf area ratio (LAR) differed significantly between the irradiance treatments (Table 3.3). It was highest in the dense shade, intermediate under moderate shade levels and lowest in full sunlight (Figure 3.4). The LAR of *C. africana* was significantly higher than that of *V. keniensis*. The supply of nutrients had no significant effects on LAR. However, seedlings of *V. keniensis* grown under high nutrient regime had higher values of LAR in all irradiance treatments (Figure 3.4). On the other hand, seedlings of *C. africana* on the same nutrient regime had lower values of LAR under moderately shaded treatments. This resulted in significant interactions between the irradiance and nutrient on one hand and the species and nutrients on the other hand. The three-way interactions (light x species x nutrient) were also significant.

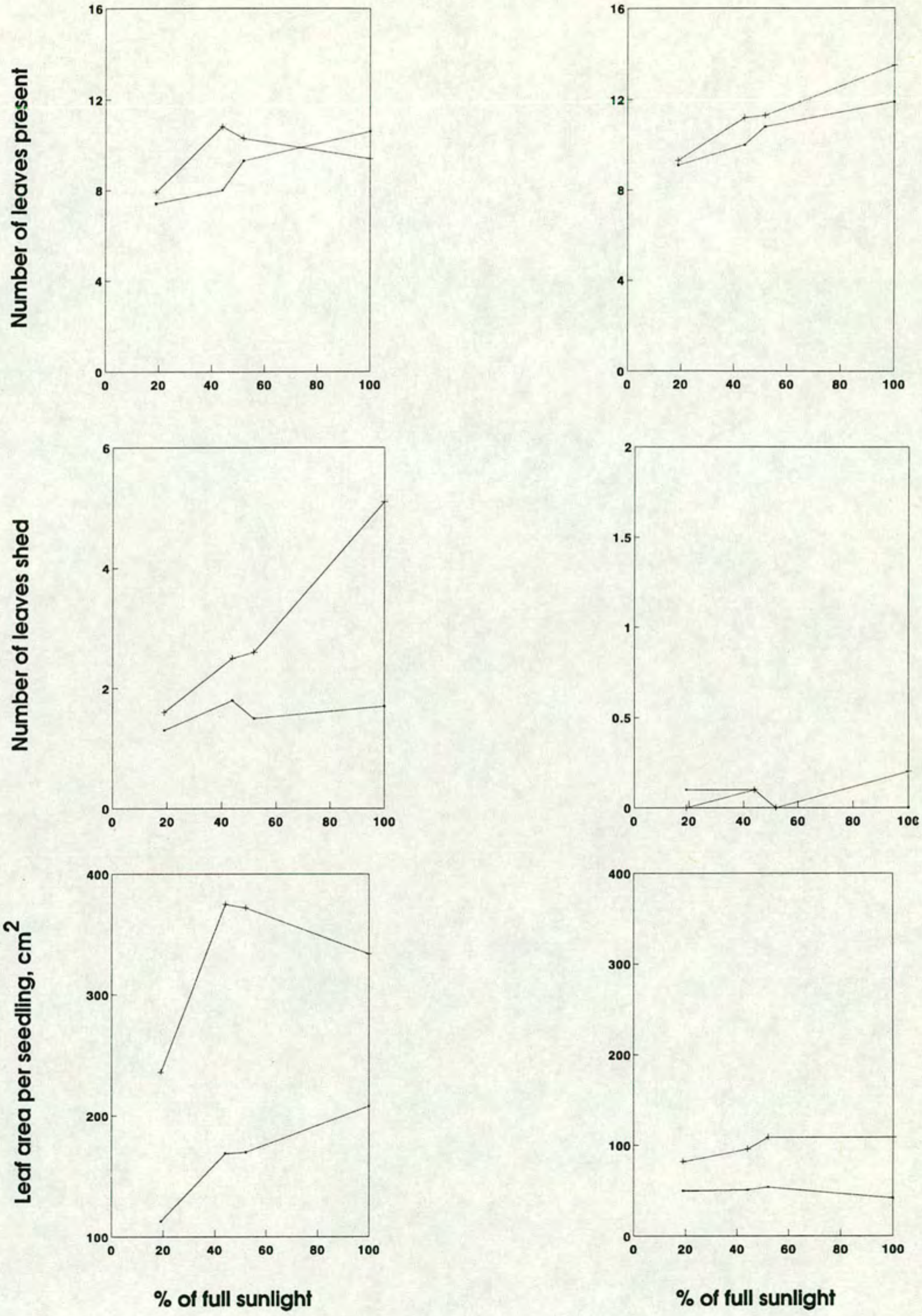

Figure 3.3. Number of leaves present, number shed and leaf area per seedling in the final harvest in *C.africana* (left) and *V.keniensis* (right) grown under low (---•---) and high (---+---) nutrient regimes and different irradiance levels.

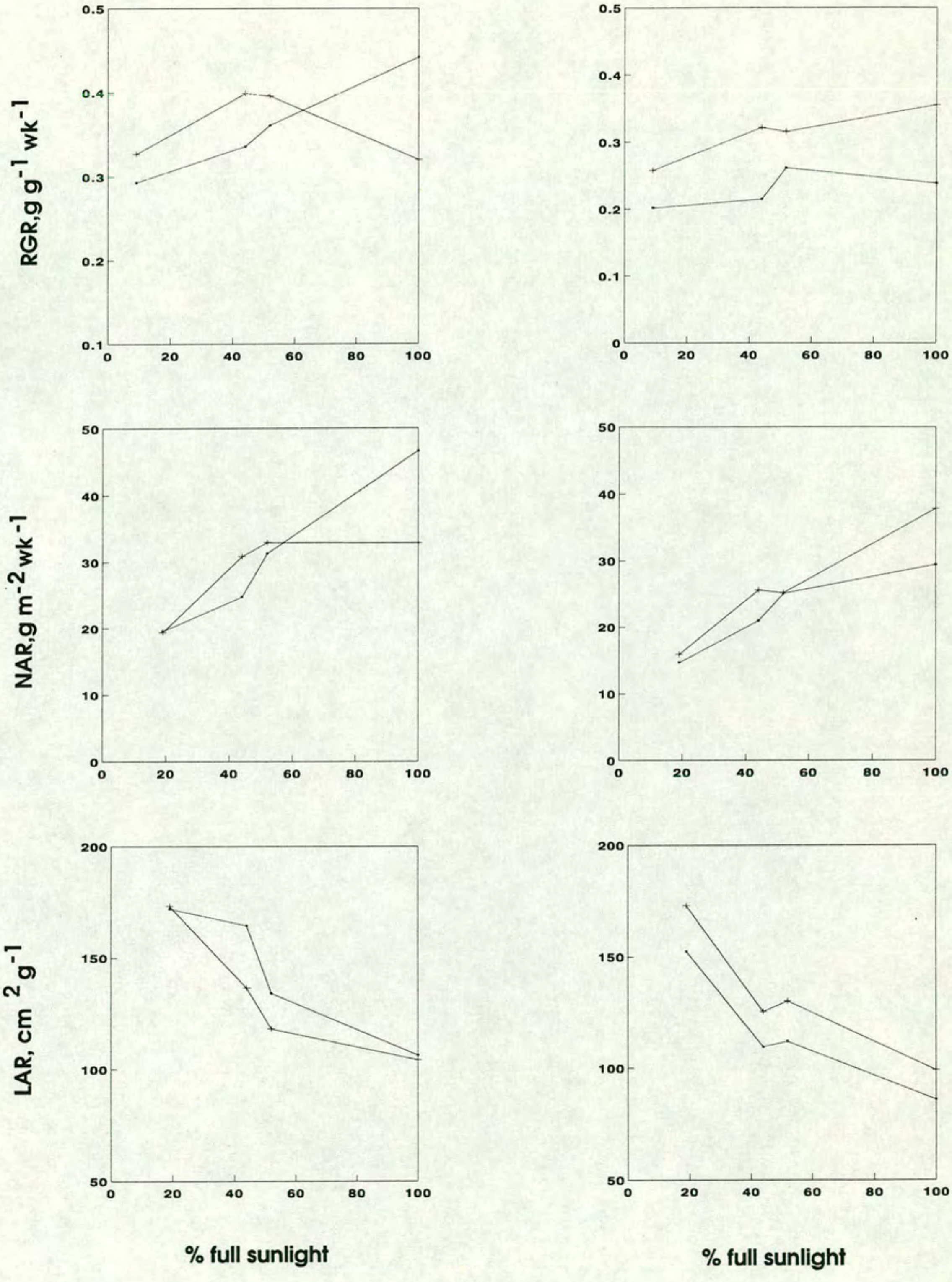

Figure 3.4. Means of RGR, NAR , and LAR of seedlings of *C.africana* (left) and *V.keniensis* (right) grown under low (---•---) and high (----+---) nutrient regimes and different levels of irradiance .

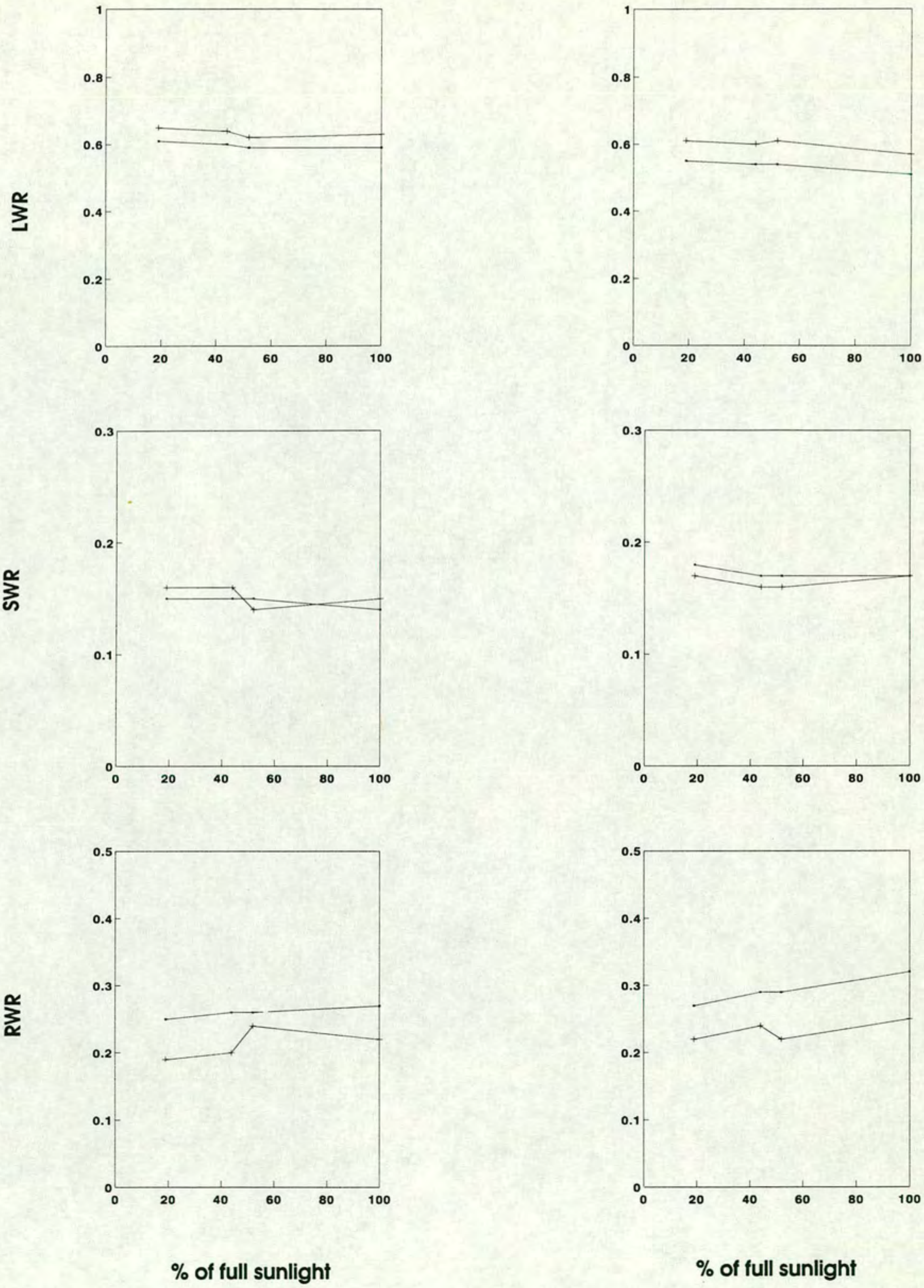

Figure 3.5. LWR, SWR, and RWR in final harvest of seedlings of ***C.africana*** (left) and ***V.keniensis*** (right) grown under low (--•--) and high (--+--) nutrient regimes and different irradiance levels.

Figure 3.6 shows that the specific leaf area (SLA) was highest in the dense shade, decreased with increasing irradiance and was lowest in the full sunlight treatment. The irradiance treatments significantly affected the SLA (Table 3.3). The SLA among the four irradiance treatments differed significantly from each other. The SLA did not differ significantly between the species but it was significantly affected by the nutrient supply. Seedlings of *C. africana* grown under high nutrient regime had lower SLA (thicker leaves) than those grown under low nutrient regime. All the interactions were significant (Table 3.3, Appendix I).

The leaf weight ratio (LWR) was not affected by the irradiance treatments (Figure 3.5 and Table 3.3) but tended to decrease with increasing irradiance. It was significantly higher in seedlings of *C. africana* than in those of *V. keniensis*. Seedlings grown under high nutrient regime had significant greater LWR than those grown in low nutrient regime. None of the interactions were significant.

Figure 3.4 and 3.6 show that the LAR had similar patterns of response to irradiance as the SLA. The LAR is a product of SLA and LWR. Since the latter was not affected by the irradiance treatments, the differences in LAR between the irradiance treatments were therefore mainly due to the effects of the SLA.

As shown in Table 3.3, the stem weight ratio (SWR) was not significantly affected by either the irradiance or the nutrient treatments. However, it tended to decrease with increasing irradiance. SWR was significantly higher in the seedlings of *V. keniensis* than in those of *C. africana*. In shaded treatments, the supply of nutrients at high level tended to increase and reduce the LWR of seedlings of *C. africana* and *V. keniensis* respectively. Although the root weight ratio (RWR) increased with increasing irradiance (Figure 3.5), it did not differ significantly between the irradiance treatments (Table 3.3). The RWR of seedlings of *V. keniensis* was significantly higher than that of *C. africana*. The nutrient treatments significantly affected the RWR. Seedlings grown in the low nutrient regime had greater RWR than those grown under high nutrients. The three-way interactions were not significant.

The pattern of response of shoot root ratio (SRR) was the opposite of RWR (Fig 3.6). It decreased with increasing levels of irradiance. However, the differences in SRR between the irradiance treatments were not significant. The SRR was significantly higher in seedlings of *C. africana* than in those of *V. keniensis*. Seedlings supplied with high levels of nutrients had higher SRR than those supplied with low levels of nutrients. None of the interactions were significant.

3.3.5 Number and Size of Leaves

The number of leaves present in the final harvest generally increased with increasing irradiance. Figure 3.3 shows that the number of leaves in seedlings grown in full sunlight was significantly higher than in all shaded treatments. Seedlings grown in the dense shade (19% sunlight) produced a significantly lower number of leaves compared to those grown under moderate shade levels (44 and 52% sunlight). Seedlings of *C. africana* had significantly higher leaf number than those of *V. keniensis*. Seedlings of *C. africana* grown in the high nutrient regime had the highest number of leaves at the moderate shade of 44% of full sunlight. Seedlings of *V. keniensis* in both nutrient regimes and those of *C. africana* in low nutrient regime, produced the highest number of leaves under full sunlight. Although the number of leaves increased with increasing levels of irradiance, leaf abscission also increased. The number of leaves shed by the final harvest was significantly higher in seedlings grown in full sunlight than in any of the shaded treatments. However, it was mainly seedlings of *C. africana* which suffered leaf loss. Seedlings of *V. keniensis* lost a negligible number of leaves in all irradiance and nutrient treatments. The number of leaves abscised in of *C. africana* increased with increasing irradiance levels. It was also greater in seedlings raised in the high nutrient regime than those grown in the low nutrient regime.

The mean leaf area per seedling peaked under moderate shade (44 and 52 % sunlight) and tended to decrease under full sunlight (Fig 3.3). It was significantly lower in the dense shade (19% sunlight) than in the other irradiance levels. The mean leaf area in seedlings grown under moderate shade levels and full sunlight did not differ significantly. The mean leaf area in seedlings of *C. africana* was about three times greater than that of seedlings of *V. keniensis*. Seedlings grown in the high nutrient regime also produced significantly greater leaf areas per seedling. There were significant interactions between the species and nutrient, species and light and among the three-way interactions. These were mainly because of the smaller mean leaf areas under high irradiance treatments in seedlings of *V. keniensis* at both nutrient regimes and in those of *C. africana* grown in the high nutrient regime.

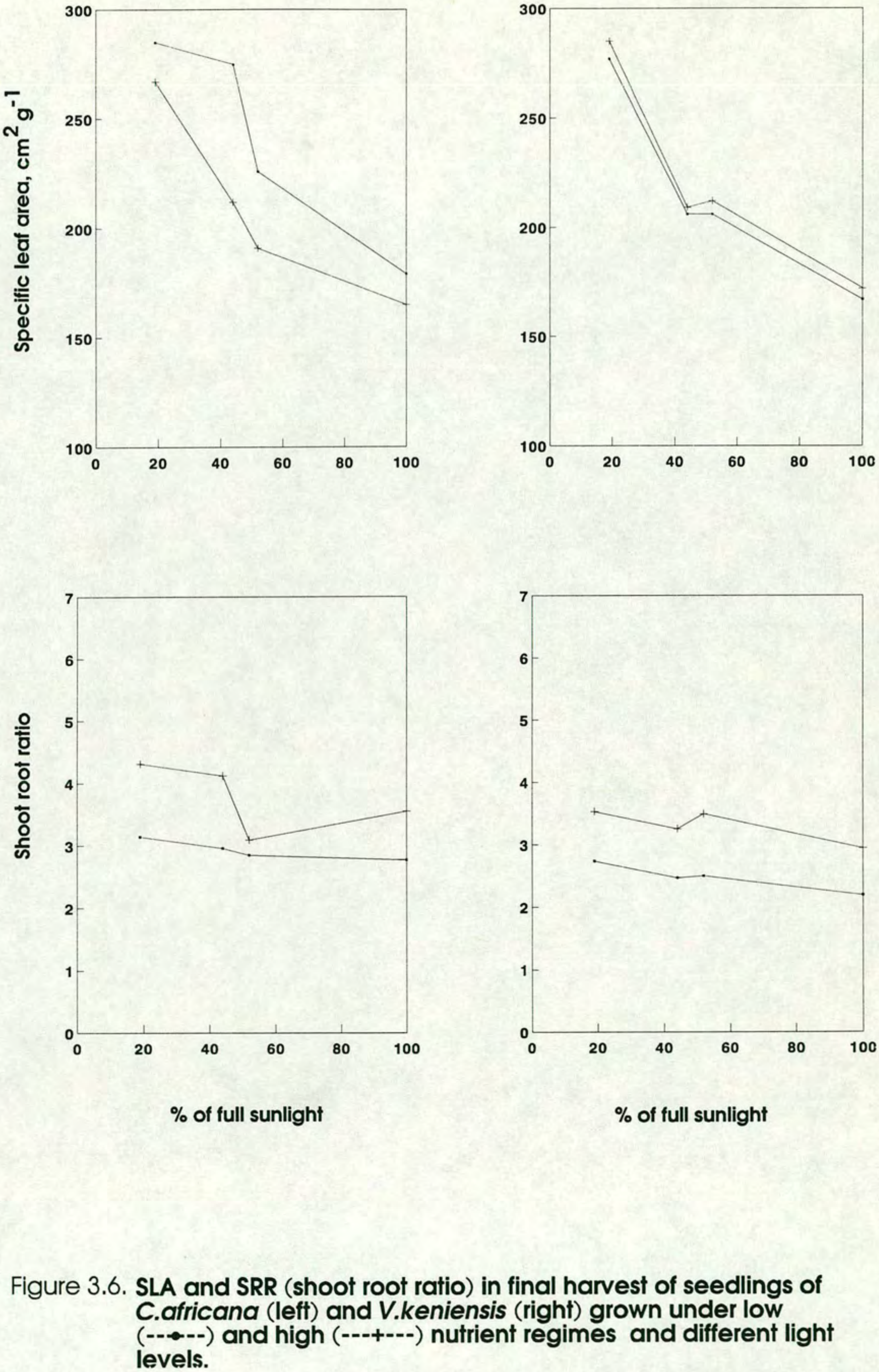

Figure 3.6. **SLA and SRR (shoot root ratio) in final harvest of seedlings of *C.africana* (left) and *V.keniensis* (right) grown under low (---•---) and high (---+---) nutrient regimes and different light levels.**

3.4 DISCUSSION

The results of the mean total dry weight, height, number and area of leaves per seedling show that *C. africana* and *V. keniensis* grow slowly under dense shade with irradiance level of 19 % of full sunlight. This level of irradiance with total daily PPFD of 7.9 mol m^{-2} d^{-1} simulates irradiance at the centre of a medium size, (approximately 400 m^2) forest gap. As shown in Figures 3.2 and 3.3, the seedlings of both species will, however, respond to increased availability of light not only in large gaps (with PPFD of 18.3 - 21.4 mol m^{-2} d^{-1}) but also under conditions of full sunlight.

Seedlings of *C. africana* showed stronger response to irradiance than those of *V. keniensis* which, however, responded moderately (Figure 3.2 and 3.3). Seedlings of *C. africana* therefore seems to be both faster growing and more light demanding than those of *V. keniensis*.

The irradiance level of maximum growth of each species was influenced by the nutrient treatments. Under low nutrient regimes, seedlings of *C. africana* seem to require full sunlight conditions for increases in dry matter, number and area of leaves per seedling (Figures 3.2 and 3.3). In contrast, seedlings of *V. keniensis* showed slow growth at low nutrients in all irradiance levels, indicating that low availability of light in the dense shade (19% sunlight) was not the limiting factor. In both species, height growth tended to be maximal under moderate shade levels (44 and 52% of full sunlight) in seedlings grown under low nutrient regime (Figure 3.2) but slightly decreased in full sun. The combination of high irradiance and low nutrients depressed height growth possibly due to a shift in allocation of biomass from the stems to the roots. This was probably necessary for maximum absorption of nutrients under the low level within the pots. The results, however, indicate that moderate shading seems necessary for better growth in height of seedlings of *C. africana* and *V. keniensis* in nutrient poor-sites.

Under high nutrient regimes, the growth of seedlings of *V. keniensis* was enhanced and increased with increasing irradiance (Figure 3.2 to 3.3). This indicates that on fertile soils, seedlings of this species require high levels of irradiance to attain maximum growth. Although seedlings of *C. africana* grown under high nutrient regimes showed better response to irradiance (in dry weight, height, number and area of leaves per seedling), maximum growth was achieved under moderate shade (Figures 3.2 and 3.3). Growth generally declined under full sunlight conditions probably due to stomatal closure.

The conclusion that seedlings of *C. africana* and *V. keniensis* grow faster under moderate shade levels is in agreement with previous observations on growth in height of seedling of some tropical trees and shrubs (Murray and Nichols, 1966; Sasaki and Mori, 1981; Oberbauer and Strain, 1985; and Kigomo, 1989).

Seedlings in these previous studies required moderate shade levels of 30-60 % sunlight for best growth in height. Fetcher *et al* (1983) reported the greatest height growth of even a pioneer species *Heliocarpus appendiculatus* under partial shade.

The RGR is a product of the NAR and the LAR (Hunt, 1978). The differences in RGR between the seedlings in the irradiance treatments were therefore due to the differences in the NAR and the LAR. As shown in Figure 3.4, irradiance had opposing effects on the NAR and LAR. An increase in irradiance increased the NAR but decreased the LAR.

Figure 3.4 shows that seedlings of *C. africana* and *V. keniensis* maintained positive RGR values which were relatively high for the dense shade (19% sunlight). The positive values were due to high LAR and positive NAR in the dense shade. However, since the irradiance level in the dense shade treatment was much higher than that normally found beneath tropical forests, the two species may not be truly shade-tolerant. Indeed, it seems probable that they are normally associated with large gaps because their values of RGR were enhanced by increased irradiance. The lack of significant differences in RGR of seedlings grown under moderate shade and full sunlight, suggests that the optimum for growth of seedlings of these species is at medium to high irradiance. Between the two species, *C. africana* displayed higher values of RGR indicating that it is faster growing than *V. keniensis*. These results provide further evidence that the dry matter accumulation in these species increases in responses to increase in irradiance.

The NAR and the RGR values in both species were comparable to those of some pioneer tropical species previously studied (Coombe, 1960; Okali, 1971 and 1972; Synnott, 1975; Kwesiga 1985; and Kamaluddin, 1991). Under full sunlight conditions, the average RGR of *C. africana* grown in both nutrient regimes was similar to that of *Trema guineensis* (Coombe, 1960) and that of *Ceiba pentandra* (Okali, 1971). The average growth rate of seedlings of *V. keniensis* in both nutrient treatments was also close to that of *Chlorophora excelsa* (Okali, 1971) and *Bischofia javanica* (Kamaluddin, 1991). The average values for seedlings *C. africana* and *V. keniensis* (for both nutrient treatments) under full sunlight treatment were higher than that reported for *Terminalia ivorensis,* a light demanding species of West Africa (Kwesiga, 1985). The positive NAR and RGR of both *C. africana* and *V. keniensis* under the dense shade (19% sunlight) is in contrast to the findings of Kwesiga (1985) for *T. ivorensis,* which displayed negative values at 25% sunlight. Popma and Bongers (1988) also recorded negative NAR and RGR in seedlings of a pioneer species, *Cecropia obtusifolia.* However, this was in a small canopy gap receiving irradiance levels of between 2.1 and 6.1% of full sun. On the other hand, the findings in the present study are in agreement with those of Kamaluddin (1991) who found positive values of the NAR and the RGR in seedlings of a gap species, *B. javanica*, grown an irradiance of 5% of full sun. Since the values of the NAR and the RGR for both *C. africana* and *V. keniensis* were moderately high at the irradiance level of 19% of the full sun, it seems that both species are likely to maintain positive values at even much lower irradiance levels.

Under full sunlight seedlings of *C. africana* grown with high nutrients, had lower RGR. This was due to several factors. First, the increased leaf abscission reduced the leaf area (Figure 3.3) and hence the LAR. Secondly, as is evident in Figure 3.4, the NAR also seems to have contributed to the decrease in the RGR, as it declined slightly after attaining a peak at 52% of full sunlight. The NAR probably did not increase because of inadequate water supply leading to stomatal closure. The roots of the larger seedlings grown in the high nutrient regime under full sunlight conditions were probably pot-bound. It is therefore likely that these larger seedlings suffered moisture stress due to impaired water-uptake, especially in the middle of the day when evapotranspiration losses were high. This problem is less likely under field conditions, but obviously availability of water can limit the growth of seedlings of *C. africana* under bright light in fertile sites.

The results of the responses of seedlings of *V. keniensis* to nutrient supply are consistent with those reported in *Flindersia brayleyana* (Thompson *et al*, 1988) and in *B. javanica* (Kamaluddin, 1991). In *F. brayleyana* seedlings grown in the low nutrient had maximal growth at medium irradiance, while those grown with high nutrients had the greatest growth under high irradiance. The combination of low nutrient and high irradiance depressed the growth. In the present experiment the responses of seedlings of *V. keniensis* were similar to those of *B. javanica* and *F. brayleyana*. The responses of seedlings of *C. africana* were, however, different from these other species in that the combination of low nutrient and high irradiance enhanced the growth, while high nutrient plus high irradiance depressed it.

In this study, seedlings of *C. africana* had a greater rate of leaf abscission than those of *V. keniensis* (Figure 3.3). High leaf turnover is one of the physiological characteristics of pioneer and secondary species (Bazzaz, 1991). Seedlings of *C. africana* therefore seem to display characteristics of a pioneer species more than those of *V. keniensis*. Leaf abscission was higher in seedlings of *C. africana* grown under high nutrient regime than those grown in low nutrient regime. This is in accordance with previous observations that plants growing on infertile sites show less leaf abscission, than those from fertile environments (Specht and Groves, 1966; Chapin, 1980). Seedlings of *C. africana* growing on fertile sites seem to show high leaf turnover, especially under full sunlight. However, the high rate of leaf abscission is likely to be an adaption to reduce water losses and not a response to increased nutrient supply.

There were large morphological differences between seedlings of *C. africana* and *V. keniensis* grown in the dense shade and in the full sunlight treatments. The values for seedlings under moderate shades levels were intermediate in response. Seedlings grown in the dense shade had thinner leaves, with SLA of about one and half times greater than that of seedlings grown in the full sun. Corré (1983a) observed that a large increase in SLA, when the LWR is generally constant, results in an increase in LAR and that this can compensate for lower photosynthesis per unit leaf area in shaded seedlings. Similar observations were also made in the present experiment. The changes in leaf morphology in *C. africana* and *V. keniensis* were similar to those of some pioneer species: *H. appendiculatus* (Fetcher *et al*, 1983), *T. ivorensis* (Kwesiga, 1985) and *B. javanica* (Kamaluddin, 1991).

Seedlings of both species adapted to dense shade by decreasing RWR and increasing allocation of biomass to the leaves and stem, as reflected by high shoot root ratio, SRR (Figure 3.6). Conversely, they adapted to the full sunlight conditions by increasing RWR and reducing allocation of assimilates to leaves and stems. Similar observations have been reported by Corré (1983a), Fetcher *et al* (1983) and Kamaluddin (1991). In response to low nutrients, there was increased allocation of biomass to roots especially under full sunlight. These results are in accordance with those reported by Chapin (1980) and Thompson *et al* (1988). This indicates that seedlings growing on nutrient poor sites are likely to have better developed roots than those growing on fertile soils. Since seedlings of *V. keniensis* also had higher RWR (and hence lower SRR) than those of *C. africana*, it suggests that they are likely to have a greater number of roots.

Increased allocation of biomass to leaves and stems in shaded seedlings is an adaptive strategy for survival which increases the photosynthetic surface and enables the plant to out-grow its competitors (Smith, 1981; Maynard and Orcutt, 1987). The low investment in root under shaded conditions is unlikely to have detrimental effects on seedlings because of the low rates of transpiration.

Increased investment in roots under full sunlight conditions and in nutrient poor sites enables the plant to exploit a larger volume of soil for water and nutrients. Low shoot root ratio has thus been used as the main criterion for selecting high quality nursery seedlings, capable of establishing fast after field planting (Sasaki and Mori, 1981). Seedlings grown under full sunlight and especially those grown under a low nutrient regime are, therefore, likely to be of higher quality than those grown under the combination of low irradiance and high nutrients.

3.5 CONCLUSIONS

Results from this study have shown that *C. africana* and *V. keniensis* are adapted to conditions found in forest gaps or clearings. *C. africana* in particular displayed typical characteristics of a pioneer species. Both species, however, are capable of maintaining net growth in dense shade (19% full sun). The light requirements of both species depend on the nutritional status of the soils. In nutrient-poor sites, growth of seedlings of *C. africana* will be higher in the open than in shaded areas. Seedlings of *V. keniensis* on the other hand do not respond to increased availability of light on infertile soils, although growth in height seems to improve when moderately shaded (at 44 and 52% sunlight).

In fertile sites, seedlings of *C. africana* will grow fast under full sunlight, but growth is likely to be limited by availability of moisture. Moderate shading seems to improve the growth of this species on fertile sites. Seedlings of *V. keniensis* on such sites grow better in the open. The two species will adapt to shading by increasing the specific leaf area (developing thinner leaves) and increasing allocation of biomass to leaves and stem. Under full sunlight, seedlings of both species produce thicker leaves with low specific area and increase allocation of biomass to roots. On poor sites, seedlings of both species also increase allocation of assimilates to roots. Although both species appear suitable for growing in the open, they are likely to benefit by moderate shading depending on the nutrient status of the soils. *V. keniensis* in particular, seems suitable for enrichment planting, but only in large forest gaps.

CHAPTER 4

LIGHT ACCLIMATION IN SEEDLINGS OF TWO TREE SPECIES IN RELATION TO NUTRIENT SUPPLY

4.1 INTRODUCTION

Seedlings growing beneath a closed forest canopy may be exposed to changes in light regimes due to formation and closure of gaps. Such gaps are usually created by naturally falling trees or branches as well as logging operations. In some tree planting programmes, nursery grown seedlings may also be exposed to changes in light regimes, for example, when shaded seedlings are planted in the open or those grown in the full sun are used in enrichment planting. In moist tropical areas, clearing stimulates rapid growth of weeds which overtop and shade planted seedlings. Any subsequent weeding in such areas expose seedlings to increased availability of light.

Gap formation or closure may vary in time and space. It is also usually accompanied by changes in other environmental variables such as temperature and atmospheric humidity. Formation of gaps or clearings result in sudden change in irradiance, temperature and vapour pressure deficits (Fetcher *et al*, 1985; Whitmore, 1985). As fallen trees or branches decompose, nutrients may also be released (Whitmore, 1985). Thompson *et al* (1988) and Riddoch *et al* (1991) have shown that leaf photosynthetic characteristics of seedlings are significantly affected by nutrient supply. This may influence the response of seedlings to changes in availability of light.

The ability of seedlings of a given species to survive and grow in response to changes in light regimes depends on their capacity to adjust or acclimate in terms of their physiology and morphology. The effects of previous light regime and season or weather conditions at the time of change may also influence the acclimation potential of the seedlings.

Few studies have been carried out on acclimation of seedlings of tropical trees to change in light availability (Fetcher *et al*, 1983; Oberbauer and Strain, 1985; Bongers *et al*, 1988; Kigomo, 1990; Turner and Newton, 1990; Popma and Bongers, 1991; Kamaluddin and Grace, 1992a, b & 1993). Fetcher *et al* (1983) compared the acclimation to change in availability of light by a pioneer species, *Heliocarpus appendiculatus* and a small gap (shade tolerant) species, *Dipteryx panamensis*. Seedlings were grown in the full sun, partial (80%) shade and full (98%) shade and switched between these light regimes. The growth of *H. appendiculatus* was found to be more plastic in response to the changes in light availability than that of *D. panamensis*. In another study, Oberbauer and Strain (1985) found that seedlings of *Pentaclethra macroloba* switched from full sun and partial shade (25% full sun) to full shade (1% full sun), displayed negative relative growth rates and suffered leaf abscission. Switching the seedlings from full shade to full sun also resulted in severe photoinhibition and leaf damage. Seedlings of this shade-tolerant species did not therefore display rapid adjustment to changes in light regimes. However, seedlings of another shade-tolerant species, *Cordia megalantha* acclimated rapidly to changes in light environment when switched between light regimes of full shade, small gap and large gap (Bongers *et al*, 1988). Popma and Bongers (1991) have also compared light acclimation potentials of three shade-tolerant Mexican species (*C. megalantha, Lonchocarpus guatemalensis* and *Omphalea oleifera*). They found that seedlings growing beneath a closed canopy displayed higher potential of acclimation to increased light availability while those growing in large gap showed lower capacity to adjust to decrease in light availability.

Kigomo (1990) studied the role of shade in establishment of seedlings of *Brachylaena huillensis* under natural conditions and under nursery management in Kenya. He found that exposure of seedlings to full sunlight resulted in damage from scorching and reduced growth and recommended gradual exposure.

Turner and Newton (1990) observed that leaves of a relatively light demanding species, *Shorea macroptera* were adversely affected by a major rapid increase in irradiance while those of another pioneer species, *Trema tomentosa*, were not. Thompson *et al* (1988) found that seedlings of *Flindersia brayleyana*, which displays a broad tolerance to a wide range of irradiance, retained latent capacity to acclimate following forest disturbance. In contrast, a light demanding *Acacia aulacocarpa* proved incapable of acclimation to shade as it failed to survive in medium and narrow gaps. Recently, Kamaluddin and Grace (1992a, 1993) examined the potential for acclimation in seedlings of a pioneer species, *Bischofia javanica*. They found that seedlings of this species have a wide acclimation potential to change in light availability that occur following formation or closure of canopy gaps.

With the exception of the study by Kigomo (1990), no investigations have been undertaken to examine acclimation potentials of seedlings of indigenous trees in Kenya. Since there is increasing interest on management of natural forests and indigenous trees in the country, it is necessary to generate information on the potentials of tree seedlings of various species to adjust to change in light regimes simulating various silvicultural systems. Little is also known on the role of nutrient supply on the ability of tree seedlings to acclimate to change in light environment. The aim of the present study is to determine the acclimation potential of seedlings of two species, *Cordia africana* and *Vitex keniensis* and how they adjust to sudden change in light availability. The hypothesis is that seedlings of these two species show a more rapid adjustment to moderate change in light availability than to extreme changes in light availability and that increased supply of nutrients enhances the adjustment process.

Seedlings in this study were initially grown under irradiance levels of 19, 44, 52 and 100% of full sun. After three months, they were transferred to irradiance levels of 13, 35, 47 and 100% of full sun. The seedlings were of two species, *C. africana* and *V. keniensis*, and were grown under low and high levels of nutrients.

4.2 MATERIALS AND METHODS

4.2.1 Treatments and Experimental Design

This experiment was also carried out at Muguga Nursery (Chapter 2). The same three types of treatments (4 irradiance levels, 2 species and 2 nutrient regimes) used in Chapter 3 were also maintained. A fourth light treatment was introduced by transferring seedlings in each of the species and nutrient combinations to four new irradiance levels. The four treatments in this experiment were therefore: 4 previous light levels (19, 44, 52 and 100% of full sun), 2 species (*C. africana* and *V. keniensis*), 2 nutrient regimes (low and high) and new or present light treatments (13, 35, 47 and 100% of full sun).

The experiment was of factorial design (4 x 2 x 2 x 4) with 64 treatment combinations. The species x nutrient x previous light combinations or sub-subplots were fully randomised within the present light treatments. The present light treatments were randomised on the experimental site, but without replications. There were 15 seedlings in each treatment combination (sub-subplot).

4.2.2 Plant Material and Nutrient Levels

A total of 960 seedlings of *C. africana* and *V. keniensis* from the experiment reported in Chapter 3 were used in this experiment. The seedlings had been grown for three months in polythene pots under two nutrient regimes (low and high) and at 4 irradiance levels (19, 44, 52 and 100% of full sunlight).

A week before the present experiment commenced, the seedlings in the high nutrient regime were top-dressed with NPK fertiliser at the rate of 3 g per seedling. The seedlings in the low nutrient regime were not supplied with any nutrients. These seedlings were generally yellow especially those of *C. africana*. They showed distinct symptoms of nitrogen deficiency except those grown at irradiance level of 19% of full sunlight.

4.2.3 Present Light Treatments and Measurements of Microclimate

The present experiment was started on 17th November 1992. In each of the four previous light treatments, seedlings in the same sub-subplots were combined in the three replicates. This gave 60 seedlings per sub-subplot in each of the four previous light treatments. The 60 seedlings in the pooled sub-subplots were randomly divided into four groups of 15 seedlings and also randomly transferred to the present light treatments of 13, 35, 47 and 100% of the full sunlight.

The irradiance levels in the present shaded light treatments were varied by use of the same three types of shade-cloth described in Chapter 3. However, the light interception differed between the occasions. This was due to the larger sizes of the shade-houses in the present experiment compared with those in the previous experiment. The larger shade-houses tended to reduce illumination. The shade-cloth was mounted on the same metal frames (Plates 4.1 and 4.2). However, three frames used in the previous experiment had to be combined to provide shade-houses of 3.0 x 2.0 x 1.0 m in length, width and height respectively. It was necessary to combine the three frames to avoid overcrowding and mutual shading among the seedlings. A ventilation gap of 25 cm was left at the bottom.

At the start of the experiment, seedlings were spaced to minimise mutual shading. They were also regularly relocated in each of the present light treatments to minimise effects of location. However, mutual shading could not be entirely avoided since some seedlings were taller than the others and the space within the shade-houses was limited. For example seedlings of *C. africana* previously grown under low and high nutrient regimes in all irradiance treatments averaged 10.5 and 16.6 cm in height respectively. On the other hand, the average heights of seedlings of *V. keniensis* grown under low and high nutrient regimes were 9.4 and 11.8 cm respectively for all irradiance treatments. The taller seedlings of *C. africana* grown in high nutrient regime therefore shaded other seedlings during some part of the day.

Measurements of PPFD, temperature and humidity were made for 7 days from 25th to 29th November and also on 13th and 14th December 1992. The instruments and procedures used were the same as those described in Chapter 2. The light quality was measured with two hand-held red/far-red ratio sensors (SKR 110, Skye Instruments Ltd., Powys, Wales, U.K). Measurements were made twice a week (for the four weeks) at about noon, local time. Simultaneous readings were made with one sensor held inside the shadehouse above the seedlings and the other held outside but at the same level.

Figure 4.1 shows the mean distribution in PPFD, air temperatures and vapour pressure deficits for the 7 days within the four present light regimes. The actual mean PPFD (in μ mol m^{-2} s^{-1}) received within the present light treatments were: 118.4, (13% of full sun); 330.2 (35% of full sun); and 443.1 (47% of full sun) and 934.5 in the full sun. The respective total daily PPFD (in mol m^{-2} d^{-1}) were: 5.1 (13% full sun), 14.3 (35% full sun), 19.1 (47% full sun) and 40.4 in the full sun. The latter was nearly the same as that recorded in the full sun of the previous light regime (Section 3.2.4). The transfer of seedlings from 19% of full sun to full sun simulated the formation of a large clearing while the transfers from either 44% or 52% to full sun corresponded to formation of a clearing in a heavily disturbed forest. Transfers from 19% to 35% or 47% simulated an increase in gap size from medium to large. On the other hand, the transfer of seedlings from the full sun to 13% of full sun was similar to planting of sun-grown nursery seedlings into medium size forest gaps.

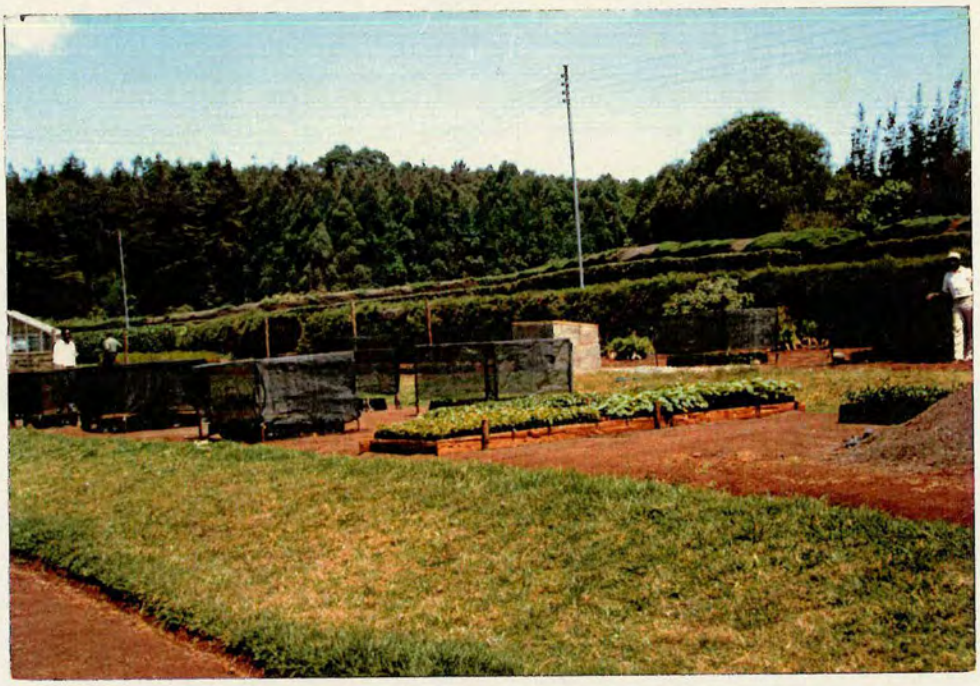

Plate 4.1: **Layout of shade-houses before the start of experiment.**

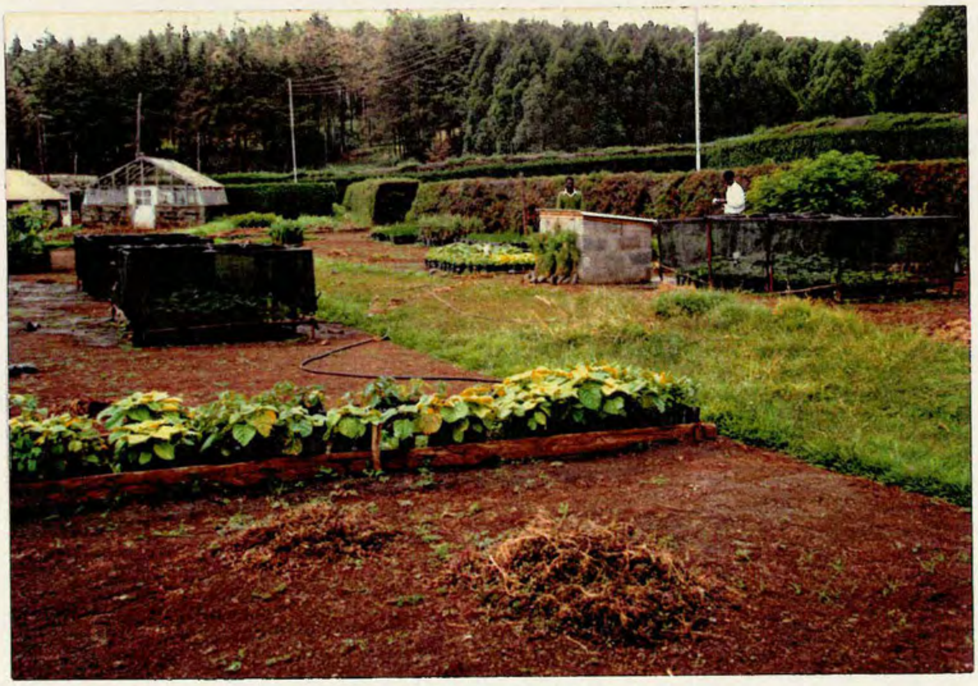

Plate 4.2: **Layout of shade-houses in the present experiment.**

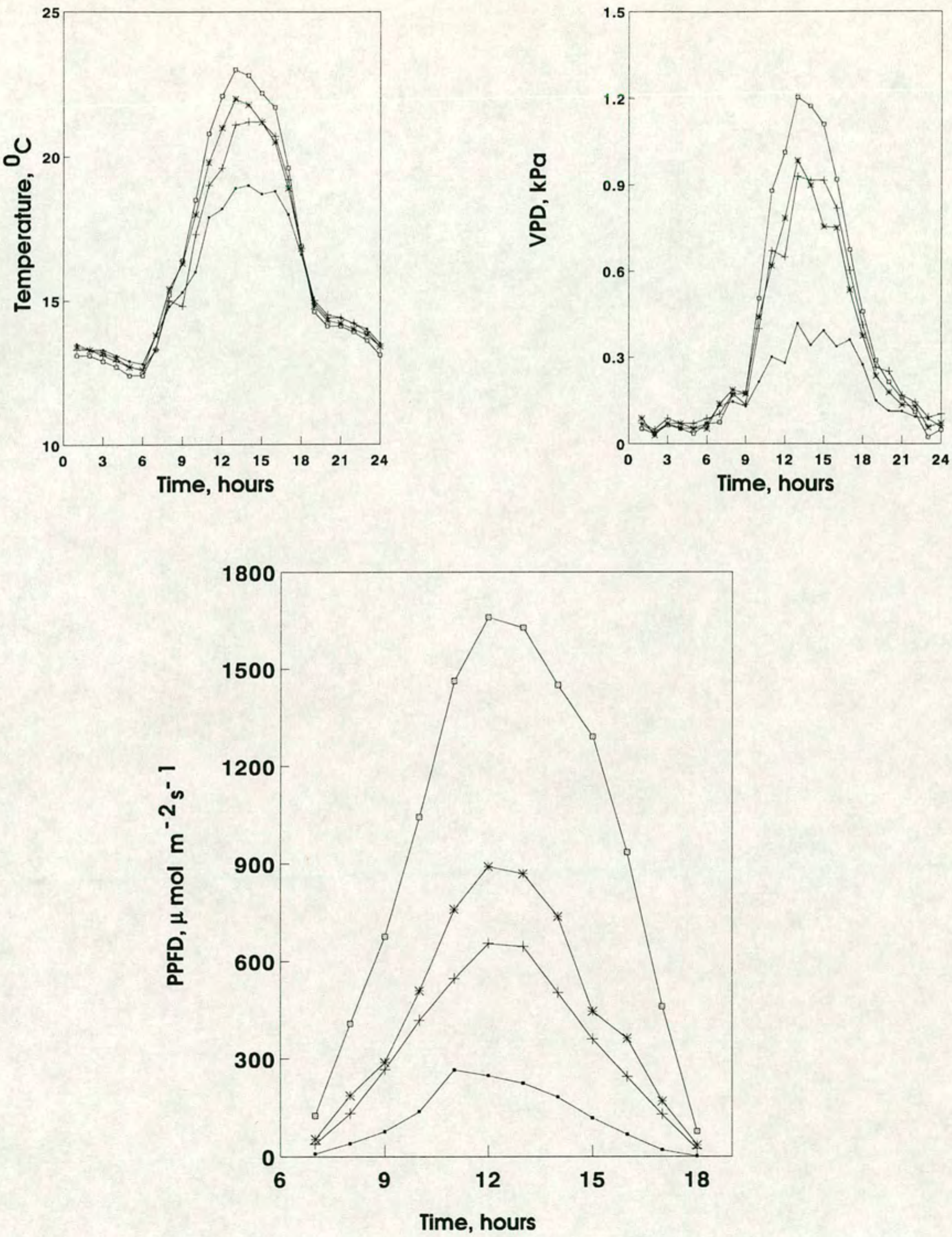

Figure 4.1. Mean daily PPFD, mean temperature and VPD within the present light treatments.

Other transfers from either 44% or 52% to 13% of full sun was similar to closure of large forest gaps. Finally, the transfer of seedlings from 19% to 13% simulated a slight decrease in the size of a medium gap.

Generally, both the previous light regime of 19% of full sun and the present regime of 13% of full sun represented dense shade. The previous light regimes of 44% and 52% of full sun and the present light regimes of 35% and 47% of the full sun also corresponded to moderate shade regimes. In this experiment, therefore, seedlings which were transferred to light regimes of 13%, 35%, 47% of full sun may generally be considered as the controls for previous light regimes of 19%, 44% and 52% of the full sun respectively. Seedlings from the previous full sun regime transferred to the present full sun were full sun controls.

The R:FR ratios received within the four present light regimes were: 1.06 for dense shade (13% full sun); 1.05 for moderate shade (35% of full sun); 1.04 for moderate shade (47% of full sun) and 1.05 in the full sun. The light quality within the present light regimes was therefore similar. Thus the experiment tested effects of irradiance, without the treatments being confounded by simultaneous change in light quality. However, in consequence the shaded treatments did not simulate natural forest shade light. The mean air temperatures (^{0}C) were: dense shade (15.4), moderate shade levels (16.0 and 16.2) and in the full sun (16.4). The temperatures recorded within the present light treatments were about the same as those in the previous light treatments. However, the mean minimum temperatures within the present light treatments were slightly higher than those recorded within the previous light treatments (Figures 3.1 and 4.1). The mean vapour pressure deficit was highest under the full sunlight treatment (0.40 kPa) and lowest in the dense shade (0.18 kPa). In the moderately shaded treatments the mean vapour pressure deficits were the same (0.34 kPa). The vapour pressure deficits in the present light regimes were therefore less negative compared to those in the previous light treatments (Figure 3.1 and 4.1). This was mainly due to the differences in weather conditions. While measurements of microclimate were carried out during the dry season in the previous experiment, this was done during the rainy season in the present experiment.

4.2.4 Data Collection and Analysis

Two harvests were made. The first one was carried out at the start of the experiment on 17th November 1992. The second harvest was carried four weeks later. The sample size was 5 seedlings per sub-subplot in each harvest. The variables assessed and procedures used were the same as those described in Section 2.3.3. Analysis was also carried out following the same methods described in Section 2.3.4.

4.3 RESULTS

4.3.1 Leaf changes

Leaf changes occurred a week after the seedlings were transferred between the light environments. Seedlings of *C. africana* transferred from the dense shade (19% of full sun) to the full sun were scorched by the sun, while those of *V. keniensis* exhibited leaf bleaching. Seedlings of both species grown under low nutrient regime were more seriously affected by exposure to full sun. By the second week, the existing leaves appeared thicker and some wrinkled. Leaflets in some seedlings of *V. keniensis* became necrotic while others had dead leaf margins. Leaf lamina re-orientation also occurred, in which the formerly flat lamina in seedlings of *V. keniensis* became V-shaped, but adopted a downward position in those of *C. africana.* Leaf-shedding and production of new leaves began also in the second week. Leaves developed in the full sun were thicker and leaf laminae had V-shape especially in seedlings of *V. keniensis*. None of the seedlings died as a result of exposure to the full sun.

When seedlings were transferred from the full sun to the dense shade (13% of full sun) the existing leaves became horizontal, thinner and more green. Leaf-shedding and production of new leaves also began in the second week. Shade-developed leaves were thin and horizontal. Leaf modifications were less noticeable in seedlings transferred from the dense shade to the moderate shade levels, or those switched between the full sun and moderate shade regimes.

4.3.2 Growth Analysis

Two-way analysis of variance showed that the effects of the present light regimes on relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) were significant (Table 4.1). The previous light regimes had significant effects on LAR only. The interactions between the previous and present light environments were not significant for the three variables.

In general, RGR increased when seedlings were transferred to environments with increased light availability and decreased when transferred to more shaded environments (Figure 4.2). It was greatest for seedlings transferred from shaded conditions to full sunlight and lowest for those transferred to the dense shade, irrespective of previous light environment. Seedlings of both species transferred from the full sun to the dense shade displayed low (and in some cases negative) values of RGR, except those of *C. africana* grown under low nutrient level. Seedlings transferred from 19% of full to 13% of full sun (dense shade control) also generally displayed low RGR. Transfers of seedlings between the dense and moderate shades on one hand, and between the moderate shades and the full sun on the other hand, generally gave intermediate values of RGR. However, the RGR of seedlings transferred to the full sun did not differ significantly from those of seedlings transferred to moderate shade levels. Seedlings of *V. keniensis* grown under low nutrient regime also displayed negative RGR when transferred from the full sun to moderate shade level of 35% of full sun. The supply of nutrients did not affect the RGR; neither did values of RGR differ between the two species. There were no significant interactions between the present light regimes, the species and nutrient treatments.

The pattern of response in the NAR was similar to that of the RGR (Figure 4.3). However, seedlings of *C. africana* grown under low nutrient level, which were transferred from the full sun to the dense shade, showed moderately high value of the NAR. Seedlings of the same species grown under high nutrient level had negative NAR when transferred from the full sun to the dense shade. Although seedlings transferred to or within the moderate shades generally gave intermediate values of the NAR, some of values were higher than those of seedlings transferred to the full sun.

LAR decreased with increasing levels of irradiance in both the present and previous light environments (Figure 4.4). Values of LAR were generally greatest for seedlings transferred to the dense shade (13% of full sun) regardless of the previous light regimes. It was the opposite for seedlings transferred to the full sun. Seedlings of *C. africana* had significantly higher LAR than those of *V. keniensis*. Also seedlings grown under high nutrient level had greater values of LAR than those grown under low nutrient levels.

Table 4.1: The effects of previous and present light regimes on growth and morphology of seedlings of *C. africana* and *V. keniensis* raised in low and high nutrients. The summary of results and details on analysis of variance are given in Appendix II and III respectively.

Parameter	Treatments				
	Present light	Previous light	Species	Nutrient	Previous x Present Interactions
Relative growth rate	*	ns	ns	ns	ns
Net assimilation rate	**	ns	ns	ns	ns
Leaf area ratio	***	**	***	*	ns
Total dry weight	**	***	****	****	ns
Height	ns	**	****	****	ns
Leaf area/plant	ns	****	****	****	ns
No. leaves present	ns	ns	****	ns	ns
No. leaves shed	ns	**	ns	***	ns
Specific leaf area	****	**	ns	ns	ns
Leave weight ratio	ns	****	****	****	ns
Stem weight	**	*	ns	***	ns
Root weight ratio	***	****	****	****	ns
Shoot root ratio	***	***	****	****	ns

ns = not significant at P<0.05;
* = P<0.05;
** = P<0.01
*** = P<0.001;
**** = P<0.0001

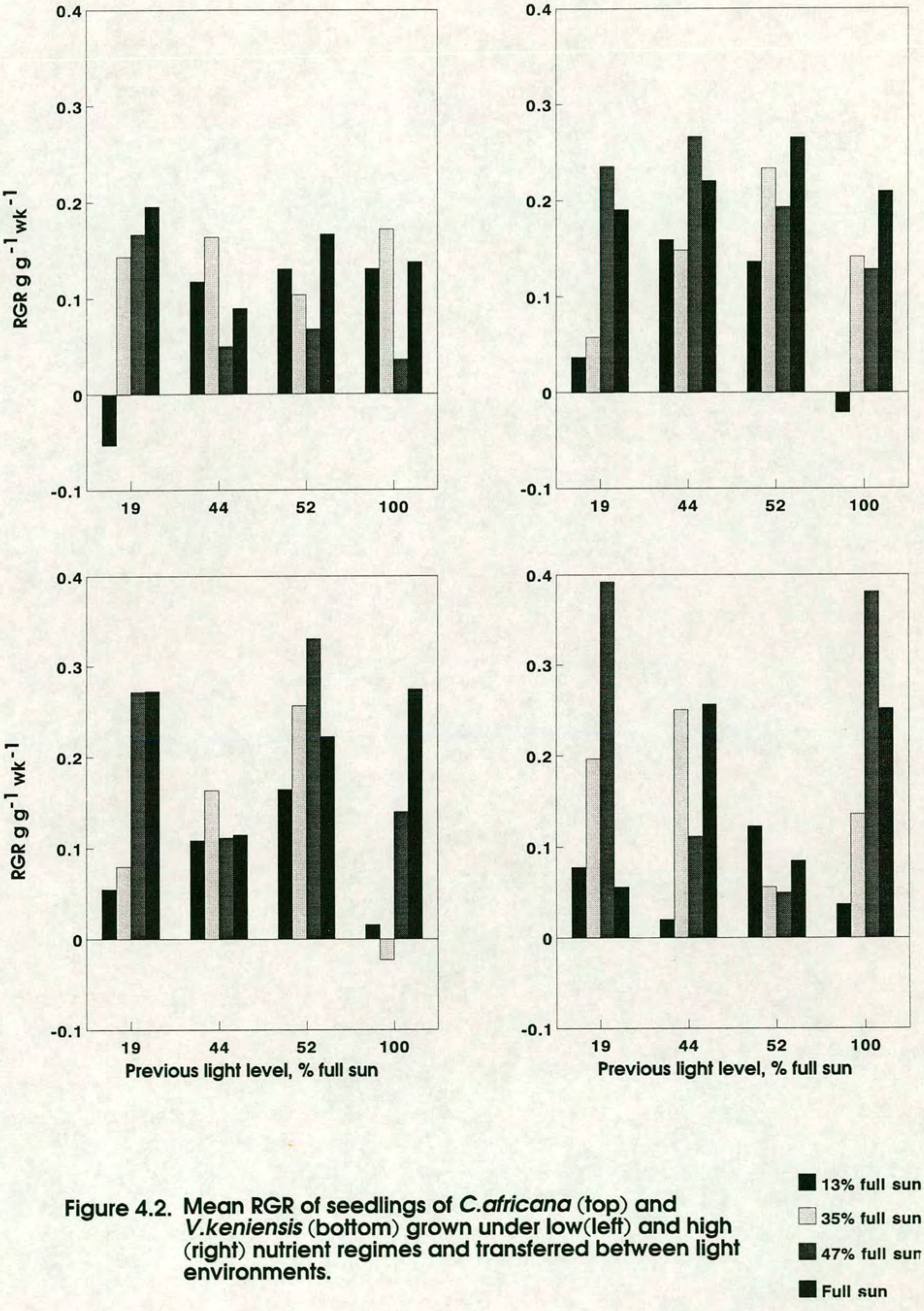

Figure 4.2. Mean RGR of seedlings of *C.africana* (top) and *V.keniensis* (bottom) grown under low(left) and high (right) nutrient regimes and transferred between light environments.

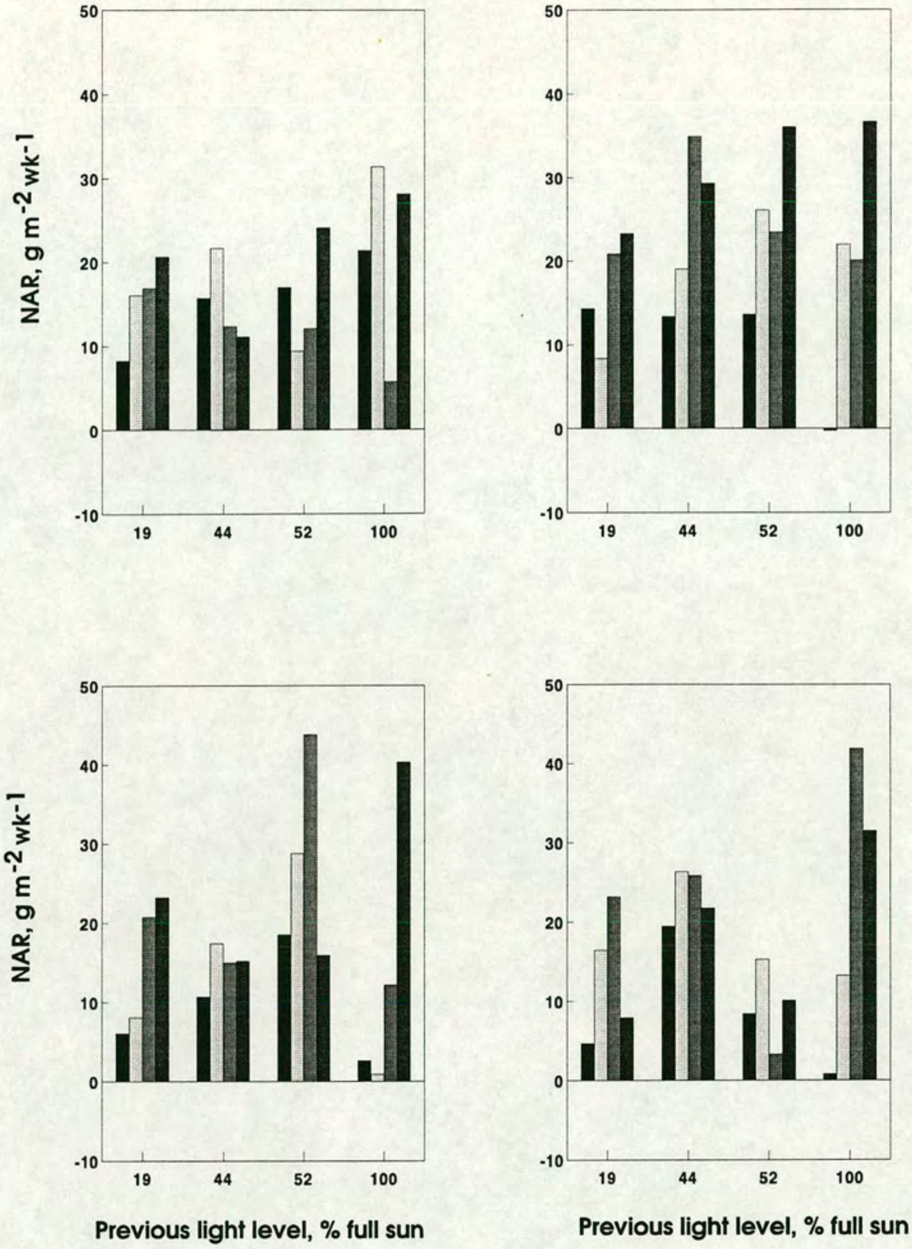

Figure 4.3. Mean NAR of seedlings of *C.africana* (top) and *V.keniensis* (bottom) grown under low (left) and high (right) nutrient regimes and transferred between light environments.

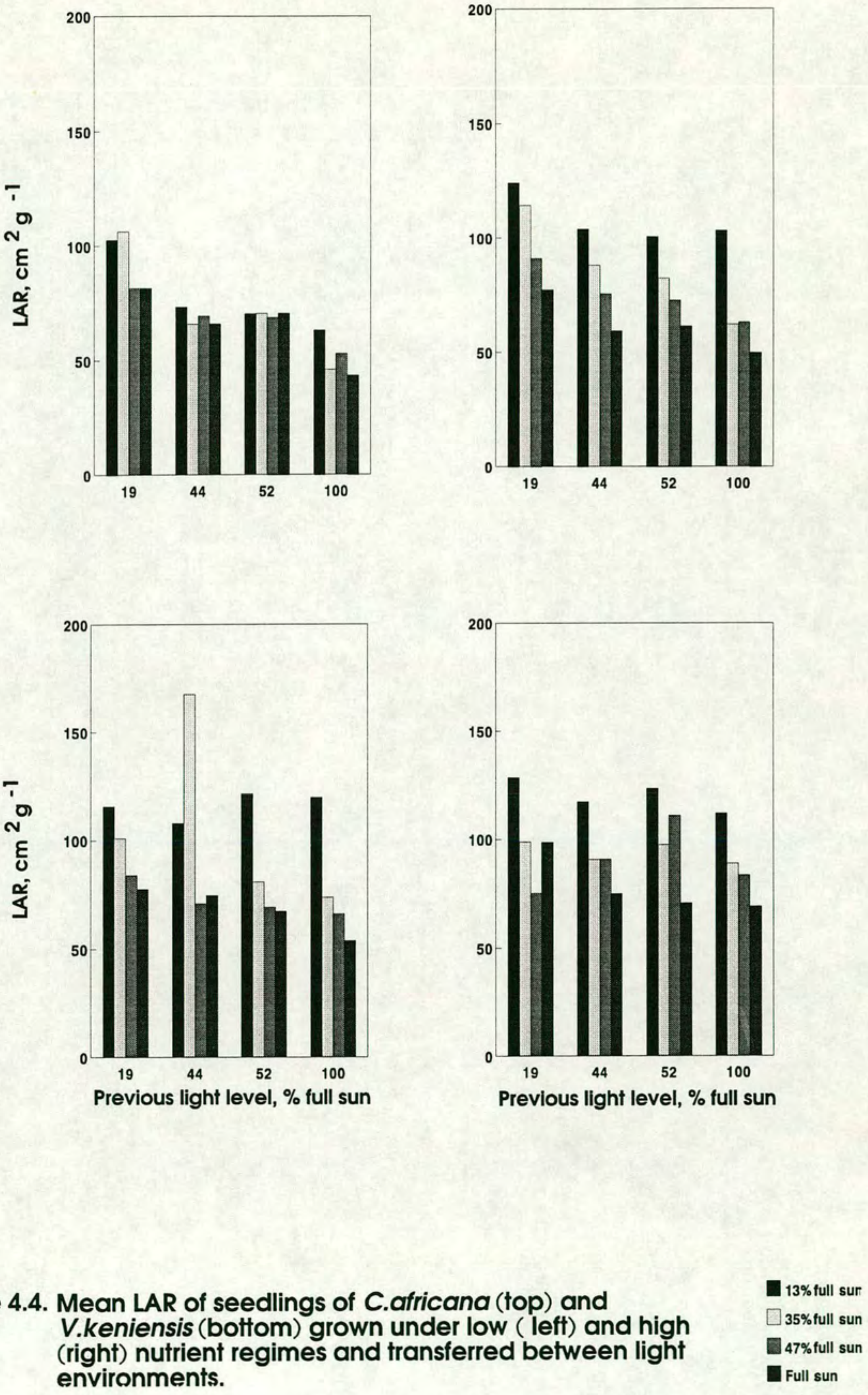

Figure 4.4. Mean LAR of seedlings of *C.africana* (top) and *V.keniensis* (bottom) grown under low (left) and high (right) nutrient regimes and transferred between light environments.

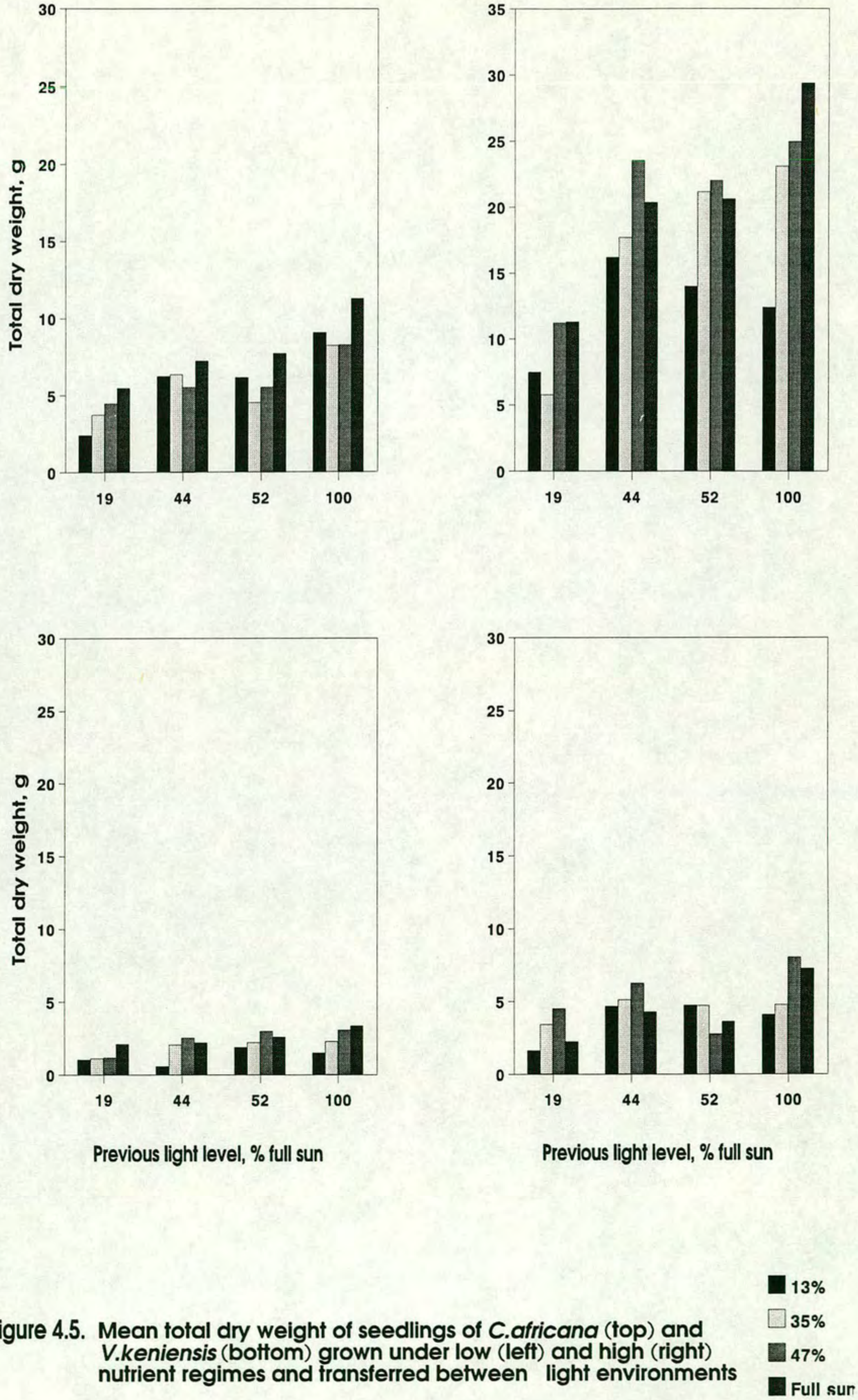

Figure 4.5. Mean total dry weight of seedlings of *C.africana* (top) and *V.keniensis* (bottom) grown under low (left) and high (right) nutrient regimes and transferred between light environments

4.3.3 Total Dry Weight and Height Growth

The total dry weight of seedlings in the final harvest increased with increasing levels of light in the present and previous environments (Figure 4.5). Both the present and previous light treatments had significant effects on the total biomass, but without significant interactions (Table 4.1). The total dry weight was greatest for seedlings transferred to the full sun and lowest for those transferred to the dense shade. Seedlings of *V. keniensis* grown under high nutrient regime did not however, follow this pattern. Seedlings transferred to moderate shade level of 47% of full sun had about the same total biomass as those transferred to the full sun. Seedlings of *C. africana* had about four times greater total dry weight than those of *V. keniensis*. Also the total biomass of seedlings grown under high nutrient regime was about two and a half times greater than that of seedlings grown under low nutrient regime. The interactions between the previous light species and nutrient treatments were significant.

The present light regimes did not significantly affect the height growth but the effects of the previous regimes were significant (Table 4.1). Seedlings transferred to the shaded conditions were slightly taller than those exposed to the full sun. Although height growth was significantly affected by the nutrient supply, the differences were mainly due to the difference in growth of seedlings of *C. africana* grown in low and high nutrient regimes.

4.3.4 Number and Area of Leaves

The effects of the present light regime on leaf area per seedling, number of leaves present in the final harvest and number of leaves shed were not significant (Table 4.1). The previous light regimes, however, significantly affected the leaf area per seedling and the number of leaves shed. Leaf shedding was highest for seedlings transferred from the full sun to the dense shade and lowest for seedlings transferred from shaded conditions to the full sun. The supply of nutrients at high level significantly increased leaf-shedding. The leaf area per seedling also increased significantly in seedlings grown under high nutrient regime.

4.3.5 Leaf Morphology

The pattern of response of specific leaf area (SLA) to changes in light environment was similar to that of the LAR (Figures 4.4 and 4.6). The SLA was significantly affected by both the present and the previous light regimes but with no significant interactions. It was greatest for seedlings transferred to the dense shade and lowest for those transferred to the full sun. Values of SLA for seedlings transferred to moderate shades were in the intermediate position. Seedlings of both species had almost similar values of SLA. The supply of nutrients showed no significant effects on this variable. However, the SLA of seedlings of *V. keniensis* grown under low nutrient tended to increase with increasing availability of light in the previous light environment.

4.3.6 Biomass Allocation

Table 4.1 shows that while the effects of the present light regimes on leaf weight ratio (LWR) were not significant, those of the previous light regimes were. The stem weight ratio (SWR), root weight ratio (RWR) and shoot/root ratio (SRR) were all significantly affected by the present and the previous light regimes. The interactions between the present and the previous light regimes were not significant.

The SRR decreased with increasing levels of the present and previous light environments (Figure 4.7). The SWR displayed similar patterns of response as the SRR. On the other hand, the response of the RWR was the opposite. The LWR decreased slightly with increasing light availability in both the present and previous light regimes.

Seedlings of *V. keniensis* had significantly higher LWR and SRR than those of *C. africana*. On the other hand, seedlings of *C. africana* had significantly greater RWR than those of *V. keniensis*. Both species had similar SWR. The supply of nutrients significantly increased the values of all parameters except the RWR. Seedlings grown under low nutrient level had significantly high RWR than those grown under high nutrient regime.

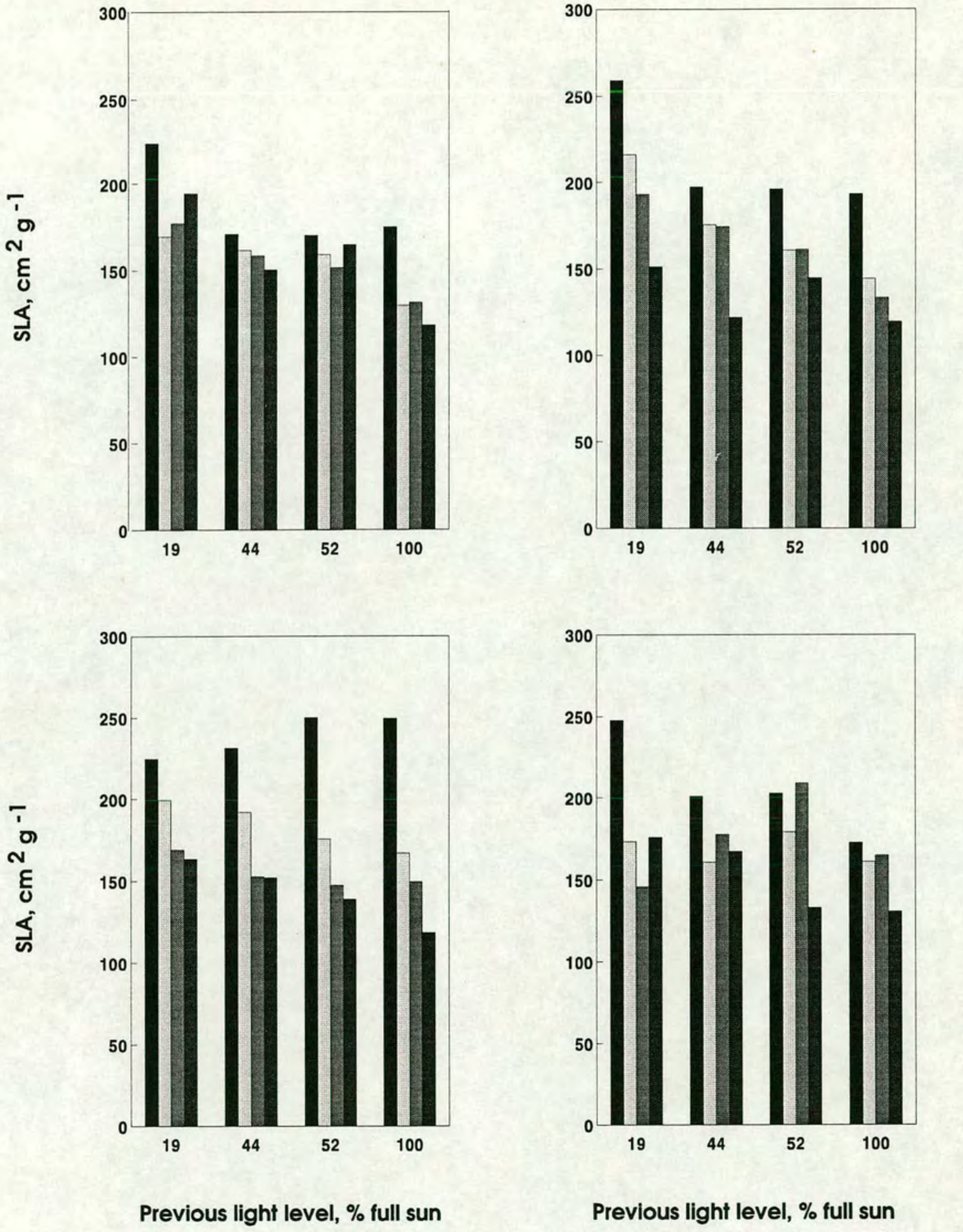

Figure 4.6. Mean SLA of seedlings of *C.africana* (top) and *V.keniensis* (bottom) grown under low (left) and high (right) nutrient regimes and transferred between light environments.

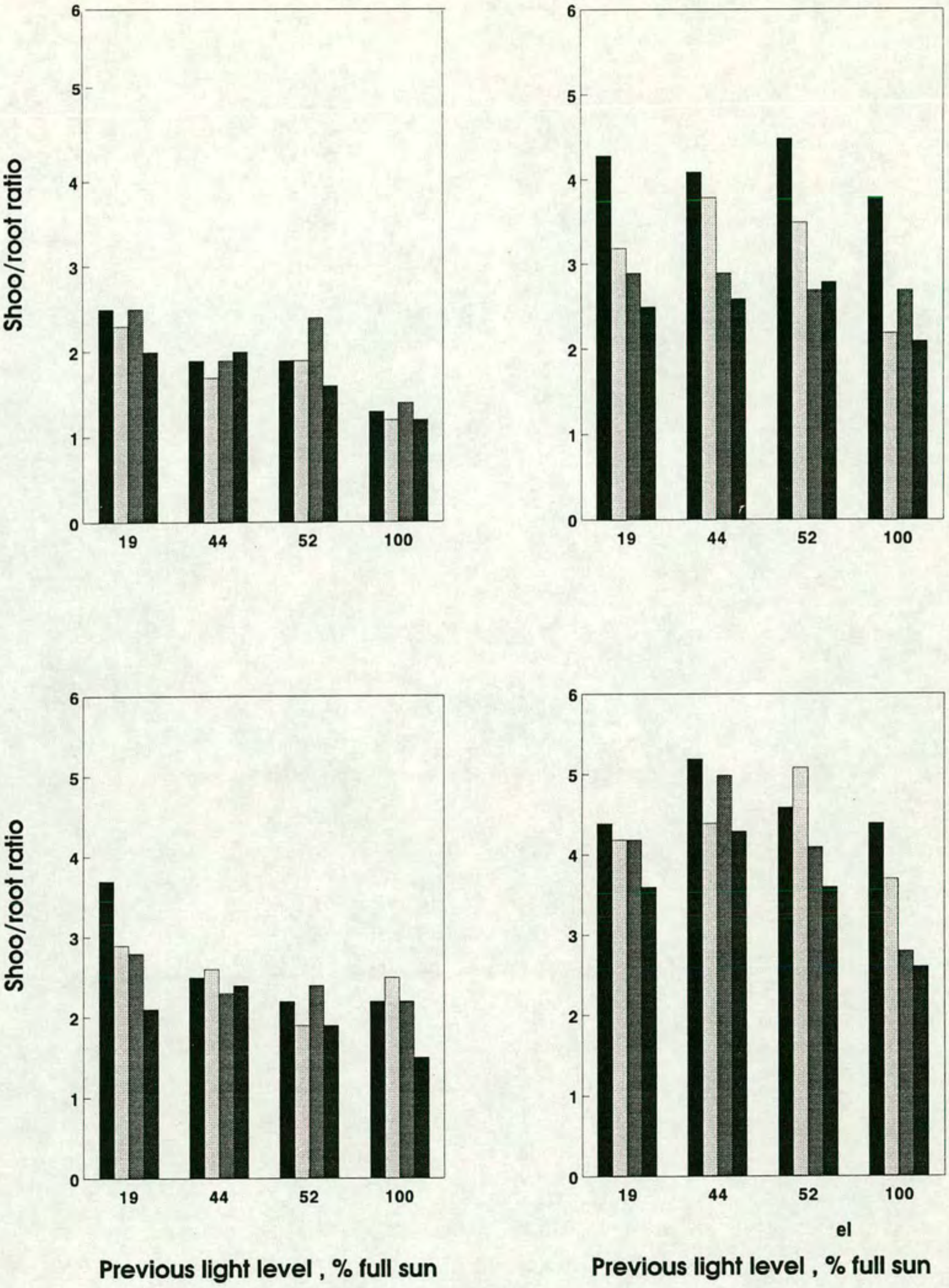

Figure 4.7. **Shoot/root ratio of seedlings *C.africana* (top) and *V.keniensis* (bottom) grown under low (left) and high (right) nutrient regimes and transferred between light environments.**

4.4 DISCUSSION

Acclimation was generally complete within a month after the transfer from one to another level of irradiance as indicated by lack of significant interactions between the present and previous light regimes in all the parameters studied. Because there were no significant interactions between the species treatments and the present light regimes, this also shows that both *C. africana* and *V. keniensis* had similar responses to changes in light availability. This was expected in *C. africana* which is usually found in open areas. Also the lack of significant interactions between the present light regimes and nutrient treatments suggest that the supply of nutrients did not influence the capacity of seedlings to acclimate to changes in the light environment. The hypothesis that the supply of nutrients enhances the acclimation process was, therefore, not supported.

The higher values of RGR in seedlings transferred to the full sun and moderate shade levels were due to the higher values of the NAR and also moderate values of the LAR (Figures 4.3 and 4.4). In seedlings transferred to the dense shade, values of the RGR were low and, in some cases, negative. This was due to the low values of the NAR and increased leaf abscission. Although values of the LAR were highest for seedlings transferred to the dense shade, these did not offset the low values of the NAR. This indicates that the NAR had no influence on the RGR when values of the NAR were low. Similar observation has been reported on seedlings of three Mexican tropical rain forest species (Popma and Bongers, 1991). Acclimation in terms of RGR of seedlings of *C. africana* and *V. keniensis* to decrease in light availability was therefore mainly through physiological adjustment, while acclimation to increase in light availability was by both physiological and morphological adjustments.

Since the seedlings transferred to the full sun and moderate shade levels displayed significantly higher values of RGR and accumulated greater total biomass than those transferred to the dense shade, this suggests that seedlings adjusted rapidly to increase in light availability and slowly to decrease in light availability. The capacity of the seedlings to acclimate to change in light availability was the same when transferred to moderate shade and the full sun regime, because their values of RGR did not differ significantly. The hypothesis that acclimation to moderate shade was faster than acclimation to the full sun was therefore not supported. However, adjustment to moderate shade was faster than to the dense shade. The results confirm earlier findings on seedlings of other tropical trees switched between environments (Oberbauer and Strain, 1985; Popma and Bongers, 1991; Kamaluddin and Grace, 1993).

Although the interactions between the present and the previous light regimes were not significant for total dry weight, it seems that acclimation with respect to this parameter was not complete. This was because the effects of the previous light environments were significant and stronger than the effects of the present light regimes. It is also evident from Figure 4.5 that the previous light regime a showed strong positive relationship with the total dry weight.

Morphological adjustment in response to changes in light availability was generally rapid, although the effects of the previous light environments were still significant at the end of the experiment. In seedlings transferred to the dense shade, the increase in LAR and its other component, the SLA, were well pronounced irrespective of the previous light treatments. Since the LWR was not affected by the present light regimes, differences in LAR were largely due to the differences in SLA.

Leaf modifications leading to thinner leaves in seedlings transferred to shaded treatments seem to have been due to spatial distribution of the plant material within the leaves, as there was no change in LWR. Modifications in which the leaves became thinner and more green with horizontal orientation were necessary adaptations to increase light interception under low light environment. However, it seems the increase in LAR in seedlings moved to the dense shade and the orientation of leaves in horizontal position also increased self-shading resulting in increased frequency of leaf abscission. However, the higher values of LAR contributed to increase in RGR of seedlings transferred to moderate shade regimes.

Transfer of seedlings to the full sun resulted in leaf scorching and bleaching. These probably associated with photoinhibition. Although leaf wrinkling indicated that some degree of damage had occurred due to sudden exposure, it was also probably due to leaf thickening and observed leaf movements from horizontal to V-shape. These changes were adaptations to reduce the excess light received by the exposed seedlings. Although seedlings transferred from the dense shade to the full sun suffered leaf scorching and bleaching, the damage was light since the seedlings seem to have recovered rapidly. This was probably because the previous light regime of 19% of full sun in the dense shade was not very low. The transfer of seedlings was also done during the rainy season, when vapour pressure deficits were low. Also, the differences in mean air temperature between the previous and present light regimes were small.

The LWR, SWR and shoot/root ratio or SRR, increased in seedlings transferred to the shaded conditions and decreased for those exposed to the full sun. The opposite pattern was observed in RWR and this indicates that transfer of seedlings to the shaded environment resulted in greater allocation of biomass to the shoots while allocation to the roots was favoured in seedlings transferred to the full sun. This explains the slightly greater height growth displayed by seedlings moved to shaded conditions. Greater allocation of assimilates to the shoots under shaded conditions will enable the seedlings to outgrow competitors. On the other hand, increased allocation of biomass to the roots in seedlings transferred to the full sun will ensure a better developed root system, necessary in absorption of water to offset increased evapo-transpiration demand under exposed conditions. Increased allocation to roots will also improve the capacity of seedlings to absorb soil nutrients.

The differences observed between the two species in some of the parameters were largely due to the carry-over effects from the previous light regimes. *V. keniensis*, however, seem to show a more plastic morphological changes in responses to sudden decrease in light availability. The differences between the seedlings growing under low and high nutrient regimes were also mainly due to the carry-over effects from the previous light regimes.

The results of this study are in general agreement with earlier findings on seedlings of tropical trees switched between different light regimes. In this study, it has been shown that when seedlings are transferred to more shaded environment, the growth rates and total dry weight decreased, but increased when moved to brighter light environments. This is in accordance with the findings of Fetcher *et al* (1983); Bongers *et al* (1988), Popma and Bongers (1991), Kamaluddin and Grace (1992a, 1993). However, Oberbauer and Strain (1985), found lower RGR in seedlings of *P. macroloba* transferred from full shade to full sun. This was due to severe leaf damage in the full sun.

Leaf scorching and bleaching observed in the present study were also similar to those reported by Turner and Newton (1990) on *S. macroptera*, Oberbauer and Strain (1985) on *P. macroloba*, Kigomo (1989) on *B. huillensis* and Kamaluddin and Grace (1992a) on *B. javanica*. Fetcher *et al* (1983) and Popma and Bongers (1991), however, did not observe any scorching or bleaching in seedlings moved from shade to full sun environment. The high leaf abscission in seedlings transferred from the full sun to the dense shade also confirmed the findings of Bongers *et al* (1988) on seedlings of *C. megalantha*. However, leaf-shedding was not reported by Fetcher *et al* (1983); Kigomo (1990); Popma and Bongers (1991) and Kamaluddin and Grace (1993).

Although the effects of the present environment on height growth were not significant, seedlings moved to shaded environments were taller. Similar observation has been reported for *H. appendiculatus* (Fetcher *et al*, 1983). Kigomo (1989) also reported increased height growth in seedlings of *B. huillensis* transferred to moderate shade (50% of the full sun). The pattern of biomass allocation in terms of shoot/root ratio was also similar to that reported by Fetcher *et al* (1983) and Kigomo (1990).

The lack of significant interactions between the present and previous light regimes for all the parameters in this study was in contrast with the findings of Oberbauer and Strain (1985); Bongers *et al* (1988) and Kamaluddin and Grace (1993). Significant interactions between the present and previous environments were found by these workers probably because their previous light regimes of 1-4 % of full sun were comparatively lower than the 19% of full sun in the present study. Except for Kamaluddin and Grace (1993) whose study was based on a pioneer species, other studies were on shade tolerant species which seem to react slowly to sudden increase in light availability. Fetcher *et al* (1983) found significant interactions in several parameters in the shade tolerant *D. panamensis* and only one in the pioneer species *H. appendiculatus*. The findings in this study therefore confirm the report by Bazzaz (1991) that the pioneer species show high acclimation potentials.

4.5 CONCLUSIONS

Acclimation potentials of seedlings of *Cordia africana* and *Vitex keniensis* were similar. Adjustment of the seedlings to changes in light availability was complete within a month after the transfers were made. Seedlings of these species growing under shaded environments with irradiance level of about 19% of full sun will respond positively to formation of large gaps and clearings. On the other hand, seedlings growing under the full sun conditions will either respond slowly or negatively to decrease in irradiance to the level of about 13% of the full sun. Sun-grown nursery seedlings are therefore unsuitable for planting in medium size forest gaps under enrichment planting programmes. Acclimation to increases and decreases in light availability was mainly physiological. However, shifts in biomass allocation pattern occurred in favour of shoots in shaded seedlings and in favour of roots when seedlings were exposed. The supply of nutrients had no influence on the capacity of seedlings to acclimate. However, with increases in light availability, high nutrient supply tended to enhance the acclimation potential of seedlings of *C. africana*.

CHAPTER 5

RESPONSES OF SEEDLINGS OF *CORDIA AFRICANA* AND *VITEX KENIENSIS* TO SIMULATED VEGETATIONAL SHADELIGHT

5.1 INTRODUCTION

Changes in spectral distribution occur when light passes through vegetation canopies (Meyer *et al*, 1975; Morgan and Smith, 1981; Smith, 1981a and 1982; Lee, 1987). The red and blue light regions are selectively absorbed while most of the far-red light is transmitted through the vegetation (Smith, 1981b). As a result the photon fluence rate in the 10 nm band centred on 660 nm is reduced in relation to the fluence rate in 10nm band centred on 730 nm (Smith, 1982). The red to far-red (R:FR) ratio is a good measure of light quality in the red and far-red regions (Smith, 1981a). It is approximately 1.17 to 1.28 under full sunlight and as low as 0.1 under forest canopies (Smith, 1982; Chazdon and Fetcher, 1984a; Lee, 1987 & 1988) . In nature, changes in light quality never occur without simultaneous changes in irradiance (Smith, 1981a). Plants growing beneath vegetation canopies are therefore subjected to light environments low in both photosynthetic photon flux density and R:FR ratio. Under low R:FR ratios, plants show marked changes in developmental patterns, particularly internode elongation (Morgan and Smith, 1981). The responses by plants to low R:FR are strongly believed to be under the control of the photoreceptor phytochrome (Morgan and Smith, 1981; Smith 1981b). Phytochrome perceives changes in the proportion of light in the red and far-red wavelengths and triggers metabolic and developmental adjustments accordingly (Smith, 1981b).

Plants have been found to respond differently to low R:FR ratio and their differences seem to be related to their ecological adaptations. Studies on temperate herbs show that species from open habitats are more responsive to changes in R:FR than those which typically grow in vegetational shadelight (Smith, 1981a; Corré, 1983b). In shade intolerant species, lowered R:FR ratio promotes stem elongation (Morgan and Smith, 1981; Smith, 1981a) and favours internode extension at the expense of leaf development (Smith, 1982). Because of increased stem elongation, shade intolerant species show higher stem weight ratio and correspondingly lower leaf weight and leaf area ratios (Corré 1983b). Rapid stem extension in shade intolerant species is a shade avoidance strategy. Under shaded conditions, this would enable them grow faster and overtop competitors.

Only a few studies have been carried out on responses of seedlings of tropical trees to light quality e.g. Sasaki and Mori (1981), Kwesiga and Grace (1986), Kwesiga *et al* (1986), and Kamaluddin (1991). In their study, Sasaki and Mori (1981) showed that in seedlings of *Shorea ovalis* grown under forest canopy, internode elongation was stimulated, but root growth was restricted. Kwesiga and Grace (1986) found that seedlings of the shade tolerant *Khaya senegalensis* were unaffected by changes in R:FR ratio while those of the light demanding *Terminalia ivorensis* were considerably affected. The specific leaf area in seedlings of *T. ivorensis* increased under low R:FR ratio and resulted in enhanced relative growth rate. Hoad and Leakey (in press) found that shoots of stockplant of *Eucalyptus grandis* grown at low (0.4 and 0.7) R:FR ratios were longer, with greater internode length, than those grown at high (3.5 and 6.5) R:FR ratios. They also observed that the specific leaf area and the proportion of dry weight as stem were significantly greater at low R:FR ratios. However, low R:FR did not promote stem elongation. Photosynthesis may also be influenced by the quality of light. Higher rates of photosynthesis have been reported in shade-grown leaves of tropical trees when the R:FR ratio was typical of shade (Kwesiga *et al*, 1986). Differences in response to R:FR ratio have also been reported between seedlings of the pioneer species *Anthocephalus chinensis* and those of the shade tolerant species *Hopea odorata* (Kamaluddin, 1991). While the stem extension increased with decreasing R:FR ratio in seedlings of *A. chinensis*, this was not observed in those of *H. odorata.* Seedling of *A. chinensis* grown under low R:FR also showed high stem weight ratio (SWR), but low leaf area ratio (LAR) and leaf weight ratio (LWR). Warrington *et al* (1988) investigated the effects of simulated shadelight and daylight on growth, development and photosynthesis of shade intolerant *Pinus radiata,* moderately shade tolerant *Agathis australis* and shade tolerant *Dacrydium cupressinum*. They found that reduction in R:FR enhanced stem elongation and increased dry matter allocation to stem and leaves in seedlings, plantlets and rooted cuttings of *P. radiata*. In contrast, the increases in stem elongation were relatively less for the other two species.

In the previous experiments (Chapters 2 and 3), the irradiance was varied, but the spectral composition within the shaded treatments varied from 1.04 to 1.06. In nature, however, a reduction in irradiance is always associated with a decrease in R:FR ratio. Vegetational shadelight was therefore not well simulated in the previous experiments. The aim of the present study is therefore to examine the effects of different levels of light quality (R:FR ratios) and irradiance on growth and morphology of seedlings of two important trees in Kenya. The two species are associated with forest canopy gaps or clearings. Two experiments were carried out under semi-controlled nursery conditions at Muguga. The hypothesis is that a reduction in R:FR ratio results in marked stem and internode elongation in these species, as a shade avoidance strategy. *C. africana* is expected to show a stronger response to changes in R:FR ratio than *V. keniensis* since it is more light demanding.

5.2 EXPERIMENT 1: RESPONSES OF SEEDLINGS TO DIFFERENT RED/FAR-RED RATIOS

5.2.1 MATERIALS AND METHODS

5.2.1.1 Plant Material

The plants used in this experiment were raised from seeds. Seeds of *C. africana* were collected in January 1993 from Shinyalu, Western Kenya. Seeds of *V. keniensis* were from the same batch (KFSC 431045/91) as those used in the experiment reported in Chapter 3. The seeds were sown on 18th February 1993 in seedbeds with sand as the germination medium. Germination commenced three weeks later and transplanting was done after 6 weeks on 29th March 1993.

Seedlings were transplanted into polythene pots which were 6.5 cm in diameter and 20.3 cm in length with capacity of 0.67 litres. These pots had drainage holes at the bottom. Transplanting was done in a timber shed with irradiance level of about 25% of full sun and R:FR ratio of about 1.04. At the time of transplanting, the seedlings had one to two true leaves. All dead and unhealthy seedlings were replaced within a week. The pots were filled with a soil mixture having similar ingredients as those described for the high nutrient regimes in Chapter 3. These ingredients were forest top soil, 6.4 mm gravel, "mycorrhizal" soil and cow manure which were mixed in the ratio 5:1:1:1 by volume respectively. NPK fertiliser was added to this mixture at the rate of 1.49 grams per litre or about one gram per pot (0.20 g N, 0.04 g P and 0.08 g K per seedling). Half-way during the duration of the experiment, the seedlings were top dressed once at the rate of one gram per seedling.

5.2.1.2 Red:Far-Red Ratio Treatments

The R:FR ratio treatments were obtained by use of 4 types of strand filters (Strand Filters, Strand Lighting, Middlesex, U. K.). Sheets of the filter material were used to cover timber frames to provide screen-houses for the seedlings (Plates 5.1 and 5.2). The filters were dark green No. 424, moss green No. 422, pea green No. 421 and medium grey No. 210. The latter was originally meant to be neutral filter control but this was later found not to be so. Each frame was 73 x 73 x 75 cm in length, width and height respectively. The top and the sides of each frame were covered with the filter material except for a ventilation gap of 15 cm at the bottom. The filter sheets were secured to the timber frames with staples and thumb pins. Each screen-house accommodated 72 seedlings (36 of each species). Because the pots were 20.3 cm long and the ventilation gap was 15 cm, the base of the seedlings was about 5cm above the ventilation gap.

Three weeks after transplanting, on 20th April 1993, the seedlings were removed from the timber shed and randomly assigned to the filter screen-houses. The screen-houses were in the open space previously used for conducting other experiments reported in Chapters 3 and 4. At the start of the experiment, seedlings of *C. africana* averaged 3.3 cm in height while those of *V. keniensis* were 3.8 cm. Seedlings of both species had produced 2 - 3 leaves above the cotyledons.

The screen-houses were tilted during watering. They were kept clean by regularly washing off the dust and soil particles. Seedlings were rearranged every 10 days to randomise effects of location within the screen-houses. The 4 types of filter materials did not show any sign of fading up to the end of the experiment.

5.2.1.3 Measurement of Microclimate

The R:FR ratios within the screen-houses were measured using 2 hand-held 660-730 ratio sensors (SKR 110, Skye Instruments Ltd., Powys, Wales, U. K.). Instantaneous readings (total of 175) were taken for 6 days in May/June 1993. During the measurements, one sensor was held above the seedlings inside the screen-house and the other was held outside at the same level. The sensors were interchanged half-way between the readings in each pair of measurements. Data on photosynthetic photon flux density (PPFD), temperature and vapour pressure deficit (VPD) were collected for 10 days (3rd - 9th May and 19th - 21st May 1993) using the same method and procedures as described in Chapter 2.

Table 5.1 gives a summary of values of R:FR ratios, PPFD, temperature and VPD within the filter screen-houses. The diurnal variations in PPFD, temperature and VPD under the four R:FR ratio treatments are also shown in Figure 5.1. Under the full sunlight conditions, the R:FR ratio was about 1.10 while the mean PPFD was 854.9 μ mol m^{-2} s^{-1}. It was greatly reduced in the light transmitted through the dark green filter (No. 424). Although the PPFD under this filter material was about 12% of the full, the R:FR of 0.02 was considerably lower than the values which have been reported under forest canopies. Lee (1989) measured R:FR ratios of between 0.20 and 0.30 under shaded forest conditions with PPFD of 2 - 5% of the full sunlight. The value of R:FR of 0.36 transmitted through the moss green filter (No. 422) was within the range of that reported by Chazdon and Fetcher (1984) for understorey shade. The other R:FR ratios of 0.58 and 0.65 were also comparable to the values reported by the same authors for medium to large forest gaps. The PPFD under the dark green filter (No. 424) simulated irradiance in a light gap of about 200 m^2 while the irradiances under the pea green and medium grey filters simulated that under large forest gaps. The R:FR ratio was closely and positively related to the irradiance.

There were small differences in temperatures within the screen-houses. The VPD was highest under the dark green filter (very low R:FR ratio). This was probably because of increased ventilation since the seedlings under this screen-house were smallest. The VPD under the medium grey filter No. 210 was the lowest probably because of errors in the wet-bulb temperature.

5.2.1.4 Data Collection and Analysis

Two harvests were made. The first was done at the start of the experiment and the second was carried out 4 weeks later. The sample size was 11 to 12 seedlings. The seedling height, number of leaves, number of internodes and leaf areas were recorded in each harvest following the methods described in Section 2.3.3. The derived variables included specific stem length, SSL (stem length per unit of stem dry weight) and internode length (Mean stem length per internode). Analysis of variance was carried out on each parameter and derived variables.

Plate 5.1: **Lay out of filter screen-houses. From left to right: pale green, moss green, medium grey and dark green.**

Plate 5.2: **Seedlings under a tilted filter screen-house.**

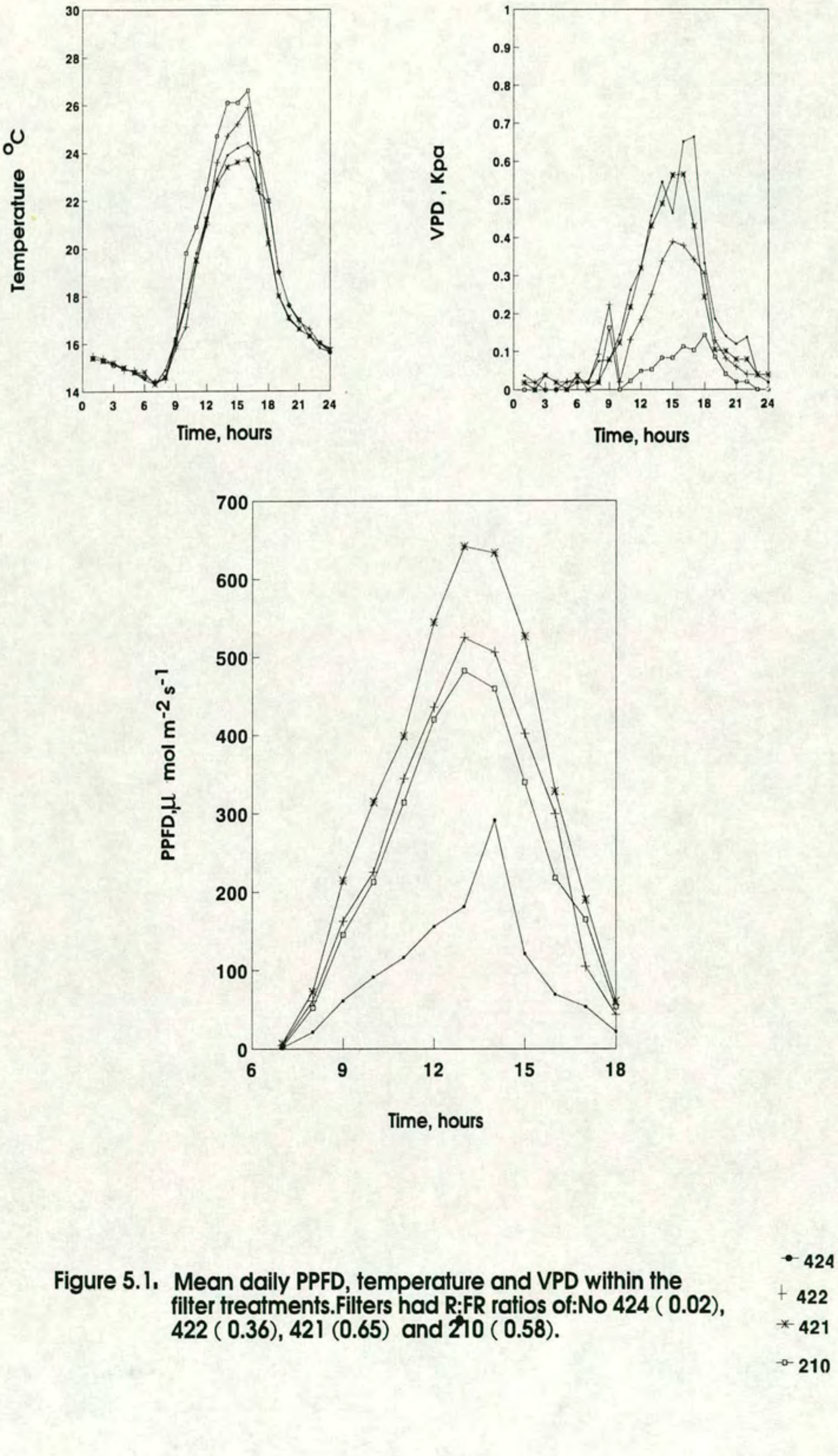

Figure 5.1. Mean daily PPFD, temperature and VPD within the filter treatments.Filters had R:FR ratios of:No 424 (0.02), 422 (0.36), 421 (0.65) and 210 (0.58).

Table 5.1: Means and standard errors of R:FR ratios, PPFD, temperature and vapour pressure deficit under the filter screen-houses

Filter type	R:FR ratio	PPFD		Temperature	VPD
		$\mu mol\ m^{-2}\ s^{-1}$	% full sun	°C	kPa
Dark green, No. 424	0.02 ± 0.002	98.8 ± 23.6	12	18.1 ± 0.7	0.20 ± 0.04
Moss green No. 422	0.36 ± 0.01	259.5 ± 53.4	30	18.2 ± 0.7	0.13 ± 0.03
Medium grey No. 210	0.58±0.02	238.6±47.4	28	18.7±0.9	0. 04±0.01
Pea green No. 421	0.65 ± 0.01	327.5 ± 64.8	38	17.9 ± 0.7	0.17 ± 0.04

5.2.2 RESULTS

A summary of results on analysis of variance of the various parameters measured is given in Table 5.2. The means and the standard errors for the same variables are also shown in Tables 5.3 and 5.4 for *C. africana* and *V. keniensis* respectively.

5.2.2.1 Growth Analysis

The effects of the simulated vegetational shadelight regimes on net assimilation rate (NAR) and relative growth rate (RGR) are shown in Figure 5.2. Table 5.2 also gives a summary of ANOVA results. In general, the responses to light quality (R:FR) and quantity (PPFD) were similar. The NAR and the RGR displayed similar pattern in response to the R:FR ratio treatments. Although the NAR and the RGR generally increased with increase in R:FR ratio, they were slightly reduced at the R:FR ratio of 0.58 (under the medium grey filter No. 210) in seedlings of *C. africana*. In both species, seedlings grown at very low R:FR (under dark green filter No. 424) showed the lowest values of the NAR and the RGR. The NAR and the RGR were significantly different in seedlings grown under R:FR ratio treatments. The differences between the species were also significant. While the NAR and the RGR were greatest under medium R:FR ratio of 0.65 (under pale green filter No. 421) in seedlings of *C. africana*, they were maximal at R:FR ratio of 0.58 in seedlings of *V. keniensis*. In the latter, the NAR and the RGR were reduced under the pea green

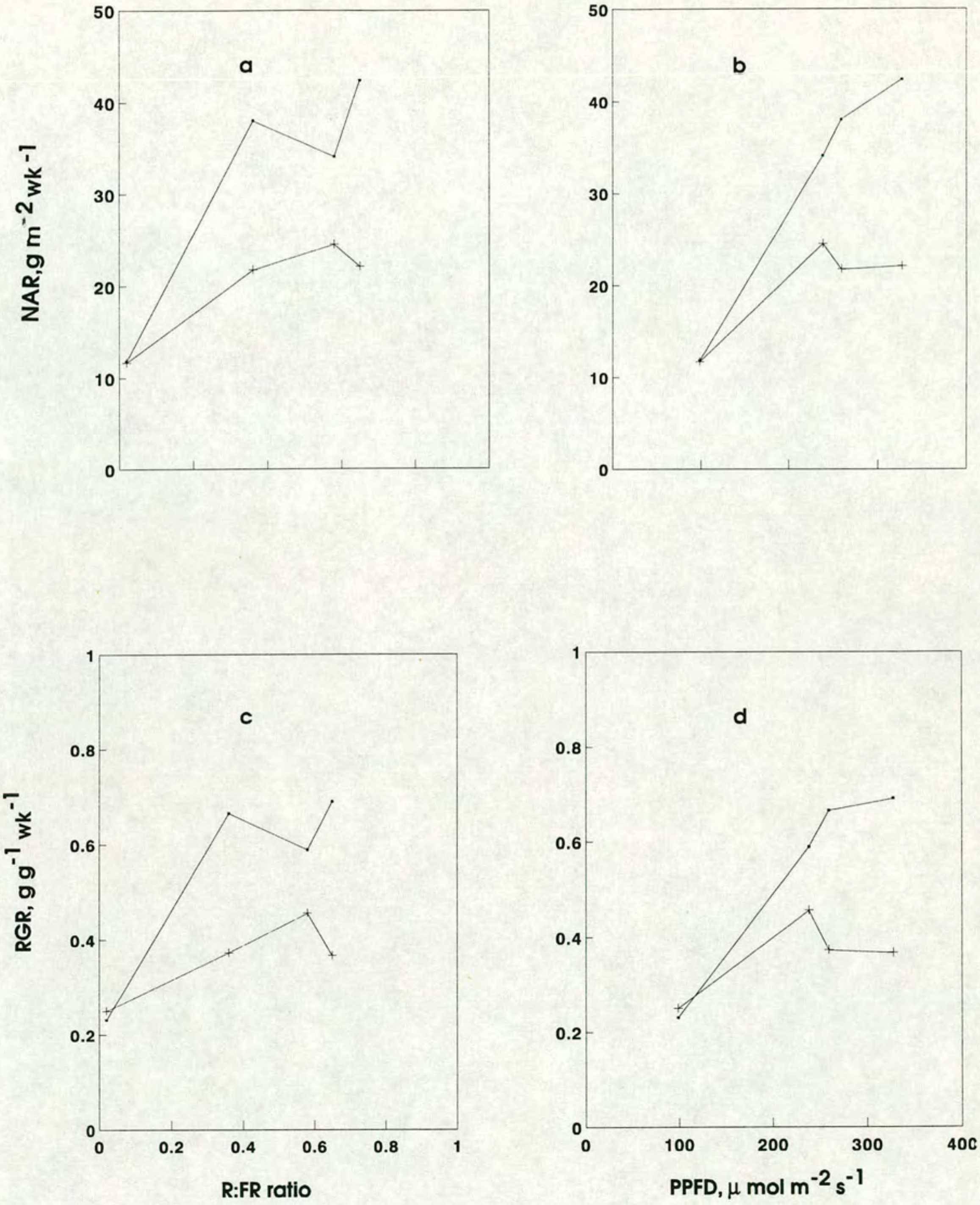

Figure 5.2 Mean NAR (a ,b) and RGR (c, d) of seedlings of *C.africana* (---•---) and *V.keniensis* (---+---) grown for under different R:FR ratios (left) and corresponding PPFD (right).

Table 5.2: Summary of ANOVA results on effects of different shadelight regimes on growth and morphology of seedlings of *C. africana* and *V. keniensis*.

Parameters	Treatments and Interactions		
	R:FR Ratio	Species	R:FR Ratio x Species
NAR	****	****	***
RGR	****	****	****
Total dry weight	****	****	****
Height	****	****	****
Specific stem length	****	****	ns
Internode length	ns	****	ns
Number of internodes	***	****	****
SLA	****	*	ns
LAR	****	ns	ns
LWR	*	ns	ns
SWR	*	*	ns
RWR	****	ns	ns

For details, see Appendix IV

Symbols: ns = not significant at P<0.05;
* = P<0.05;
** = P<0.01;
*** = P<0.001 and
**** = P<0.0001

Table 5.3: Means and standard errors of some variables in seedlings of *C. africana* grown at different R:FR ratios

Parameter/ R:FR ratio	0.02	0.36	0.58	0.65
NAR, g m^{-2} wk^{-1}	11.8±2.7	38.0±3.8	34.1±9.6	42.3±8.2
RGR, g g^{-1} wk^{-1}	0.23±0.1	0.66±0.1	0.59±0.1	0.69±0.2
LAR, cm^2 g^{-1}	268.7±22.6	191.8±24.7	213.6±47.5	175.0±18.0
SLA, cm^2 g^{-1}	446.3±43.5	329.2±52.1	363.2±59.2	335.5±22.5
Total dry weight, g	0.11±0.0	0.61±0.2	0.58±0.1	0.71±0.2
Height, cm	6.0±1.4	9.5±1.6	8.8±1.4	10.3±1.0
SSL, cm g^{-1}	225.1±30.0	86.3±12.9	83.6±16.2	76.7±10.7
Internode length, cm	1.8±0.5	1.8±0.3	1.6±0.2	1.8±0.3
Number of internodes	3.5±0.5	5.4±0.5	5.7±0.6	5.8±0.7
LWR	0.60±0.1	0.59±0.1	0.59±0.1	0.53±0.0
SWR	0.24±0.0	0.18±0.0	0.20±0.0	0.19±0.0
RWR	0.16±0.1	0.23±0.1	0.22±0.1	0.28±0.1

Table 5.4: Means and standard errors of some variables in seedlings of *V. keniensis* grown at different R:FR ratios

Parameter/ R:FR ratio	0.02	0.36	0.58	0.65
NAR, g m^{-2} wk^{-1}	11.7±1.1	21.8±4.3	24.5±6.5	22.1±6.8
RGR, g g^{-1} wk^{-1}	0.25±0.1	0.37±0.1	0.45±0.2	0.36±0.1
LAR, cm^2 g^{-1}	222.7±22.8	202.3±14.8	271.0±25.3	191.3±16.9
SLA, cm^2 g^{-1}	475.3±41.5	361.3±34.7	370.1±46.0	350.0±24.5
Total dry weight, g	0.06±0.0	0.14±0.0	0.17±0.1	0.14±0.0
Height, cm	6.3±1.2	7.4±1.6	6.8±1.6	6.7±0.1
SSL, cm g^{-1}	436.1±93.9	276.9±60.0	220.8±32.3	224.8±42.3
Internode length, cm	2.4±0.7	2.5±0.9	2.2±0.6	2.2±0.3
Number of internodes	2.8±0.4	3.1±0.5	3.2±0.6	3.0±0.0
LWR	0.57±0.0	0.56±0.0	0.60±0.0	0.56±0.1
SWR	0.26±0.0	0.24±0.1	0.20±0.0	0.23±0.1
RWR	0.17±0.0	0.23±0.0	0.20±0.0	0.23±0.0

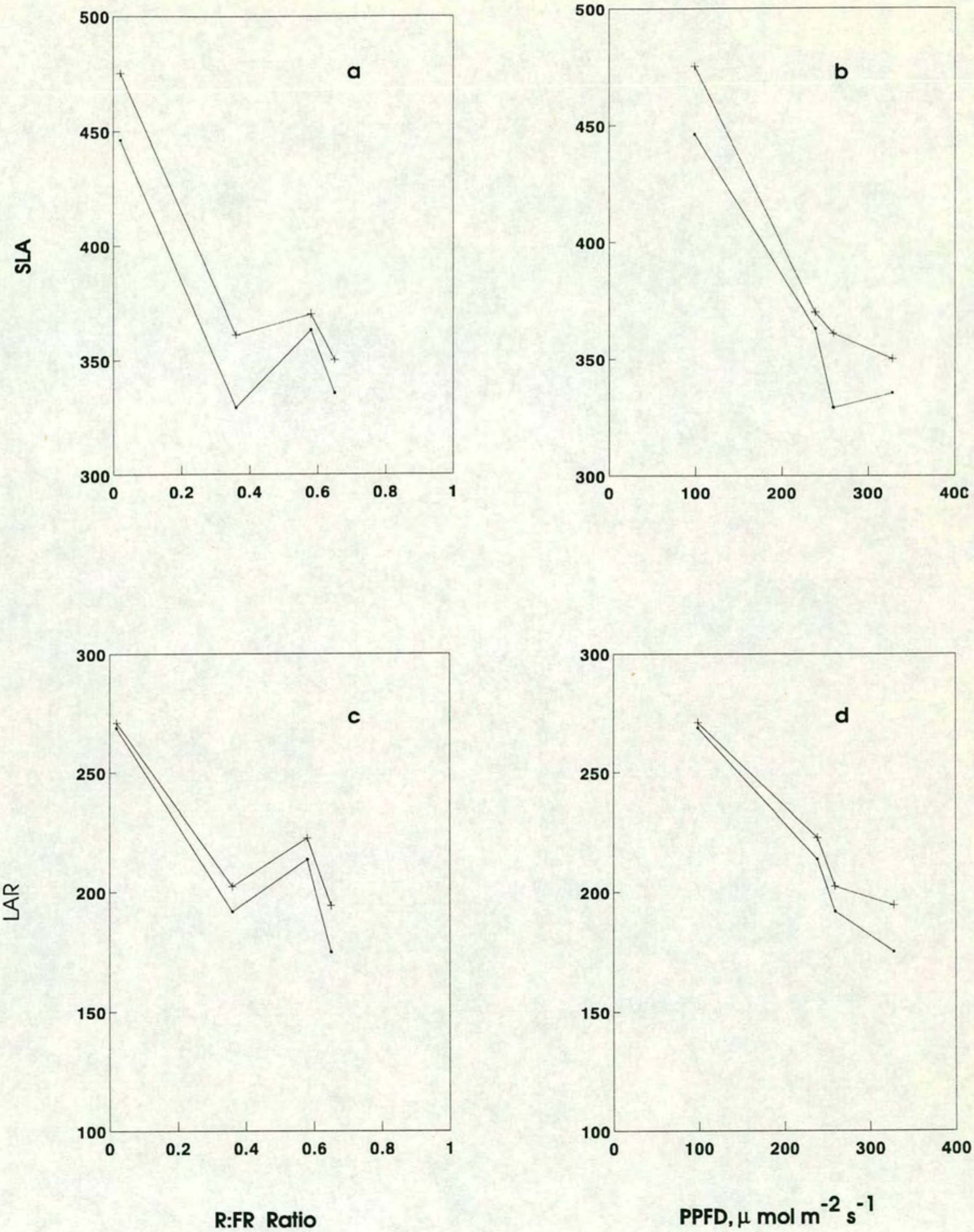

Figure 5.3. Mean SLA (a ,b) and LAR (c, d) of seedlings of *C.africana* (---•---) and *V.keniensis* (---+--) grown under different R:FR ratios and corresponding PPFD (right).

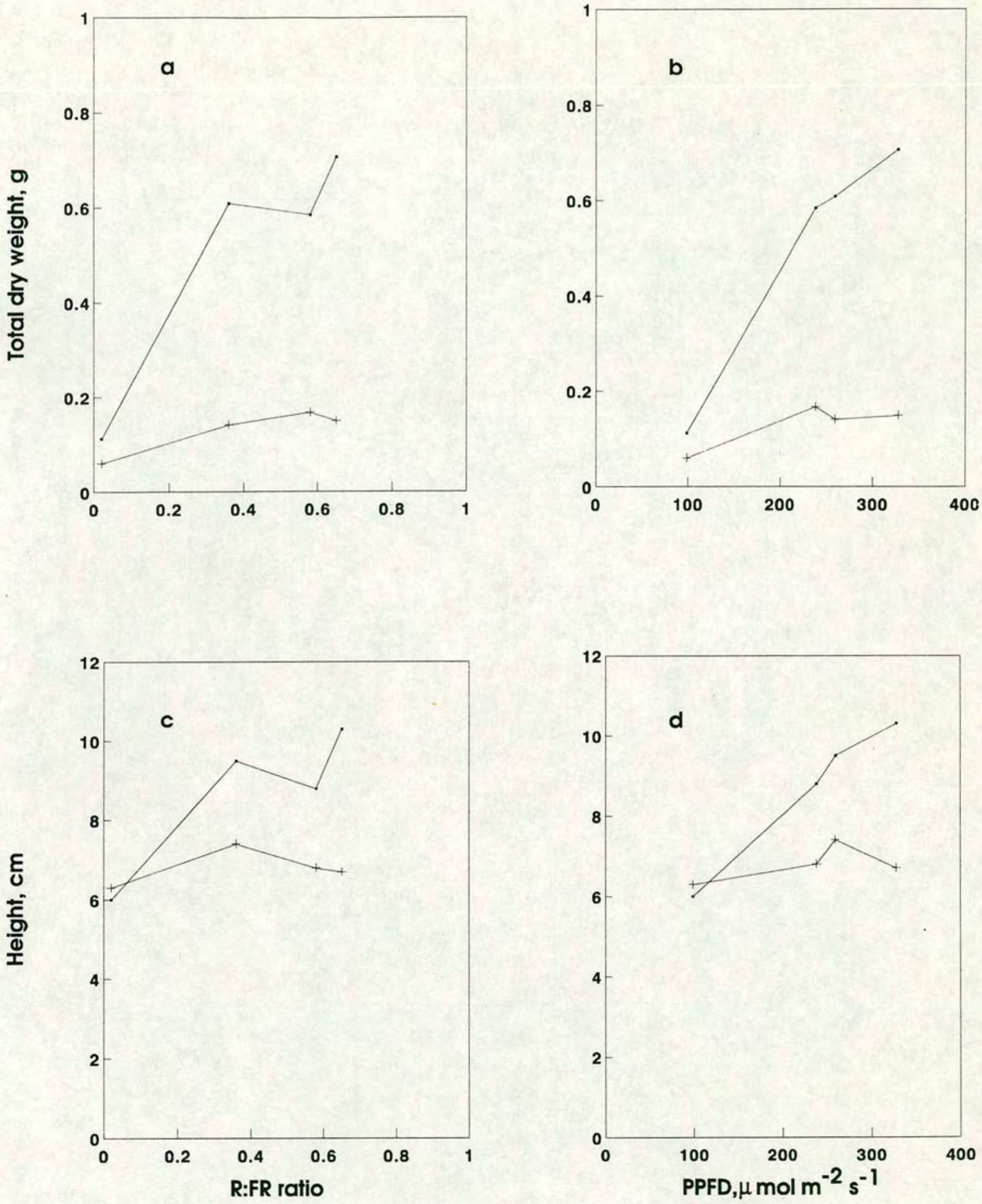

Figure 5.4. Mean total dry weight (a, b) and mean height (c, d) of seedlings of *C.africana* (---•---) and *V.keniensis* (---+---) grown under different R:FR ratio (left) and corresponding PPFD (right).

filter (R:FR ratio, 0.65). This resulted in significant interactions between the R:FR ratio and species treatments. As shown in Figure 5.3 the leaf area ratio LAR generally decreased with increasing R:FR ratio and PPFD although it increased at the R:FR ratio of 0.58. It was highest for seedlings grown at very low R:FR ratio and lowest for those grown at medium R:FR of 0.65. Significant differences were observed between seedlings grown under the different R:FR ratios. There were no significant differences between the species but the interactions between the R:FR ratio and species treatments were significant.

5.2.2.2 Total Dry Weight and Height Growth

The responses of total dry weight and height growth to shadelight treatments in the final harvest followed the same patterns as those of the RGR (Figure 5.4). The R:FR ratio treatments significantly affected both total dry weight and the height growth (Table 5.2). The differences between the species were significant, but not in all treatments as indicated by significant interactions between the R:FR and the species. With increasing irradiance, there was a large increase in total dry weight in seedlings of *C. africana* which was greatest at the R:FR ratio of 0.65 (under pea green filter No. 421). For this species, there was a moderate increase in height growth with increasing R:FR ratio. On the other hand, seedlings of *V. keniensis* displayed little response to increase in R:FR ratio in both the total dry weight and the height growth. Significant interactions were observed between the species and R:FR ratio treatments in both growth parameters.

5.2.2.3 Stem Extension

The stem extension as indicated by the specific stem length, SSL (defined as the total stem length or height per unit of stem dry weight) was significantly affected by the R:FR ratio treatments (Table 5.2). Figure 5.5 shows that in both species, the SSL generally decreased with increasing R:FR ratio and PPFD. The decrease was rapid under very low R:FR ratio (dark green filter No. 424). For both species, the SSL was significantly larger in seedlings grown under very low R:FR ratio than in seedlings grown under any other R:FR ratio treatments. No significant differences were observed in seedlings grown under low and medium R:FR ratio regimes. The differences between the species in stem extension were significant. Seedlings of *V. keniensis* had about two and a half times greater SSL than those of *C. africana*. However, both species showed similar pattern of stem extension in response to R:FR ratio treatments and interactions were not significant.

5.2.2.4 Internodes

Figures 5.5 and 5.7 show the influence of light quality and quantity on the number and length of internodes. As shown in Table 5.2, the number of internodes formed differed significantly between the R:FR ratio treatments but their lengths did not. In both species, seedlings grown under very low R:FR ratio and low PPFD had fewer number of internodes compared to those grown under other shadelight treatments. No significant differences were observed in the number of internodes formed by seedlings grown under low and medium R:FR ratio treatments. Internode length was slightly greater in seedlings grown under very low R:FR ratio but the differences were not significant. The differences between the species in both the number and length of internodes were significant. Seedlings of *V. keniensis* had fewer but longer internodes than those of *C. africana*. The interactions between the R:FR ratio and species treatments were significant in the number of internodes formed but not in the internode length.

5.2.2.5 Morphological Responses

The effects of shadelight treatments on specific leaf area (SLA) and LAR are shown in Figure 5.3. Seedlings of both species showed the same patterns of responses to shadelight in both the SLA and the LAR. The R:FR ratio treatments significantly affected the SLA. Differences between the species were also significant. In both species, however, the SLA was greater for seedlings grown at very low R:FR ratio. It decreased with increasing R:FR ratio and was lowest at medium R:FR of 0.65. The R:FR ratio of 0.58 significantly increased the SLA in comparison to the SLA of seedlings grown at either R:FR of 0.36 or 0.58.

5.2.2.6 Biomass Allocation

Both species displayed similar responses in the pattern of allocation of biomass to different plant organs (Figure 5.6 and 5.7). The R:FR ratio treatments significantly affected the leaf weight ratio (LWR), stem weight ratio (SWR) and root weight ratio (RWR) and the effects on the latter were much stronger (Table 5.2). Both species had almost the same LWR and their differences were not significant. The SWR increased with decreasing R:FR ratio. It was highest at very low R:FR ratio and lowest under medium R:FR ratio. Seedlings of *V. keniensis* showed significantly greater SWR ratio than those of *C. africana*. The RWR responded to light quality treatments in the opposite way to that of the SWR (Figure 5.6). However, no significant difference was observed between the two species in RWR. The

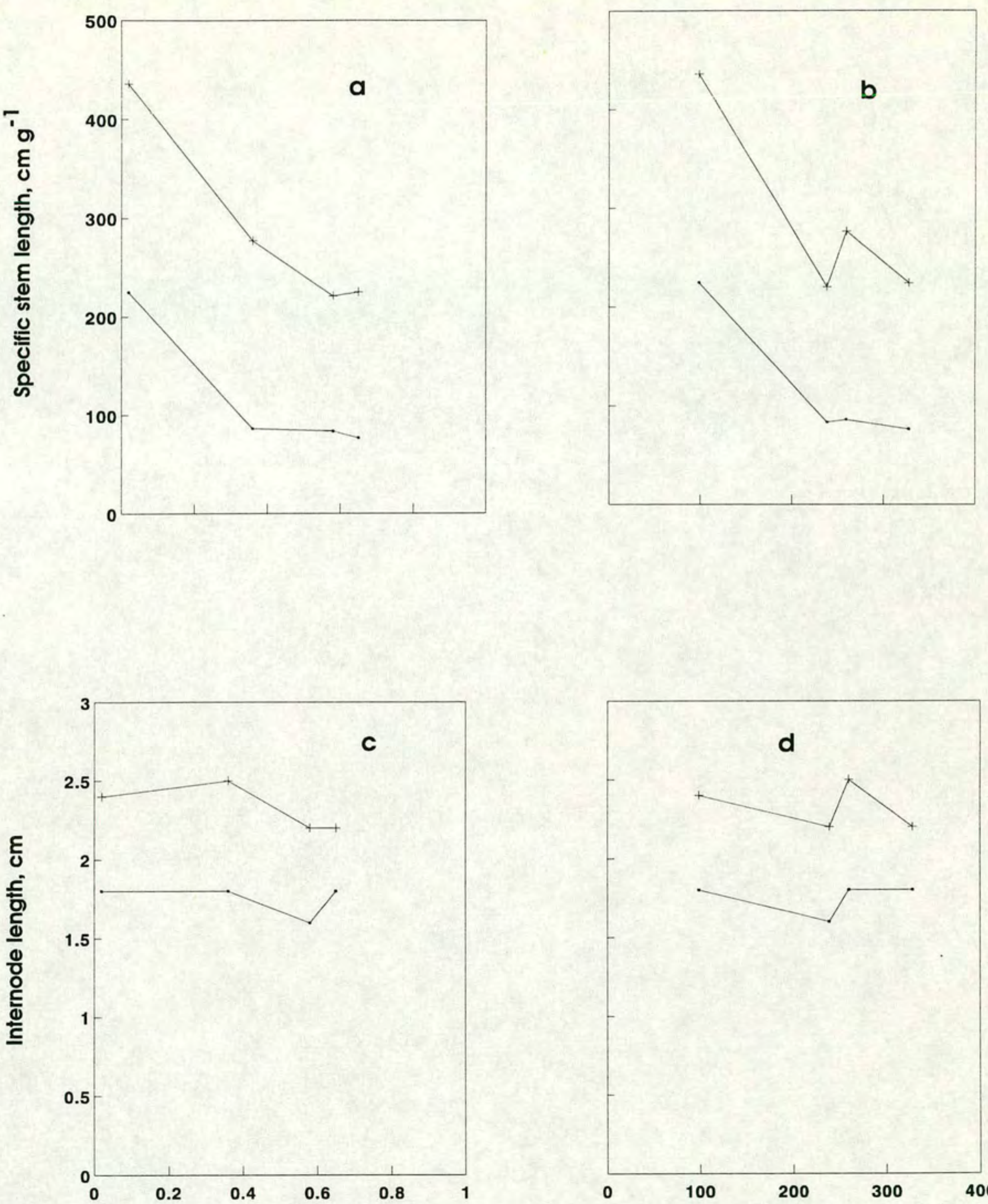

Figure 5.5. Mean specific stem length, SSL (a, b) and mean internode length (c, d) seedlings of *C.africana* (---•---) and *V.keniensis* (---+---)grown in different R:FR ratio treatments (left) and corresponding irradiance regimes (right).

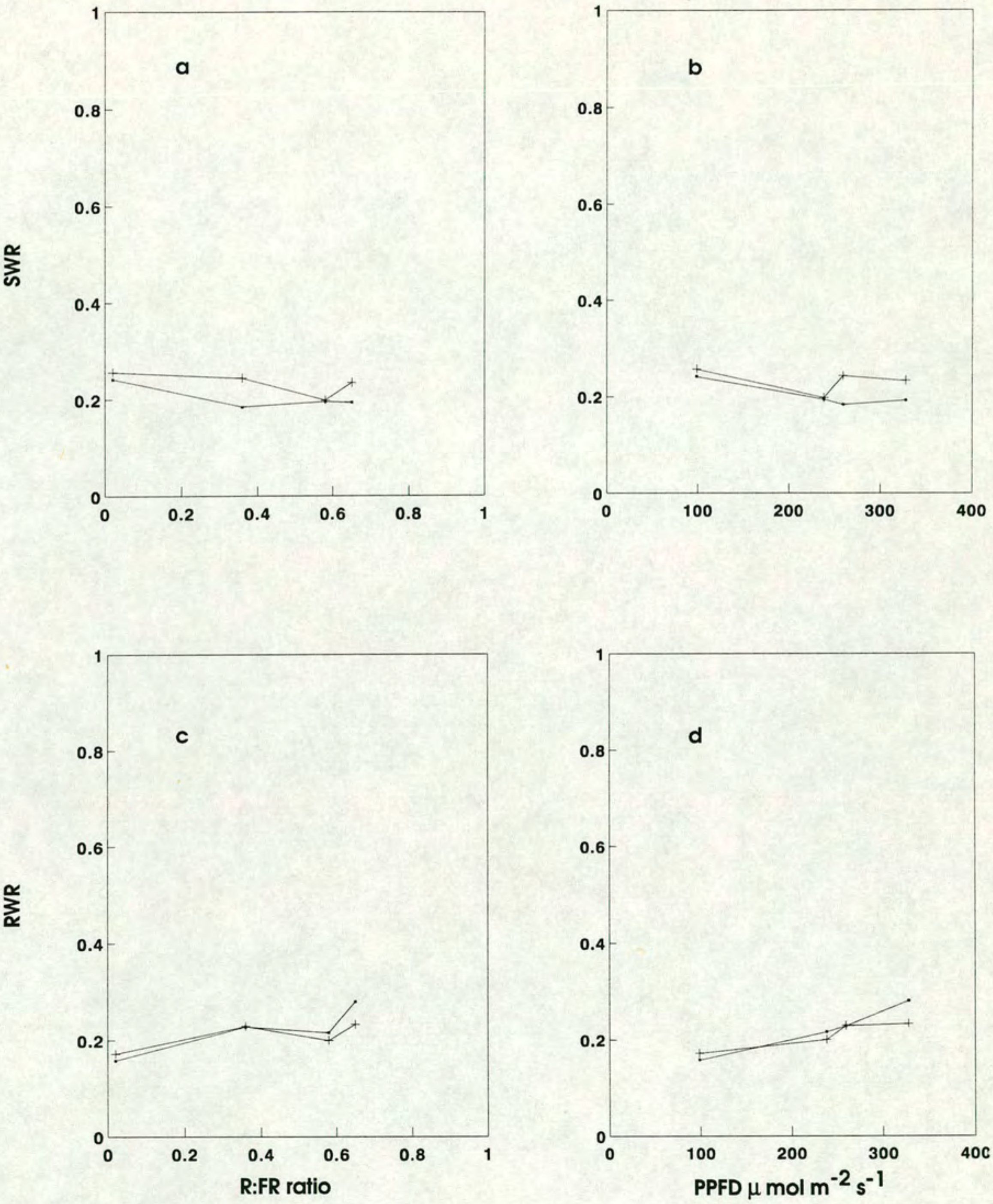

Figure 5.6. Mean SWR (a, b) and RWR (c, d) of seedlings of *C.africana* (---•---) and *V.keniensis* (---+---) grown under different R:FR ratios (left) and corresponding irradiance (right).

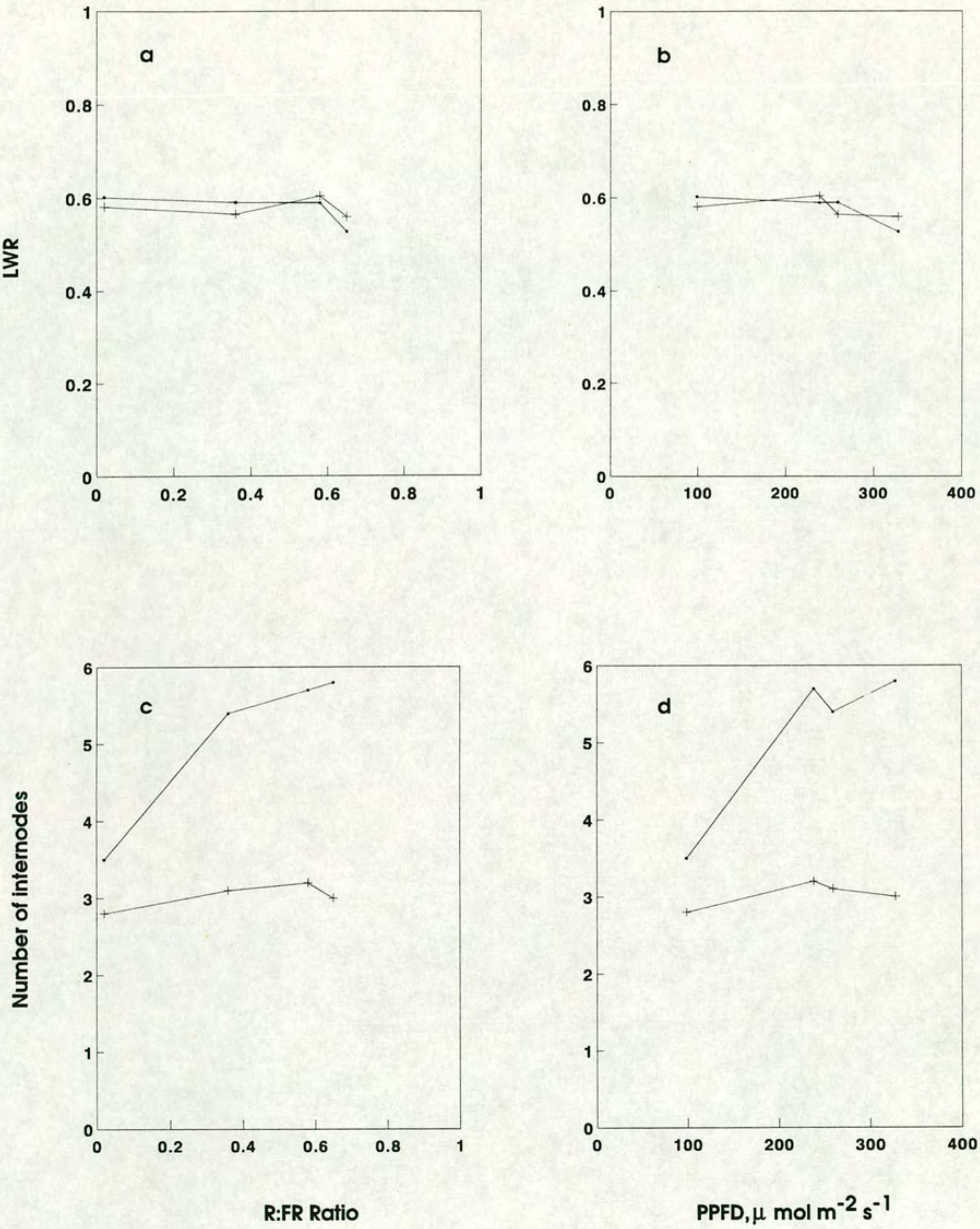

Figure 5.7. Mean LWR (a, b) and number of internodes (c, d) of seedlings of *C.africana* (---•---) and *V.keniensis* (---+---) grown at different R: FR ratios (left) and corresponding irradiance (right).

interactions between the species and R:FR ratio treatments in biomass allocation were not significant.

5.2.3 DISCUSSION

Under full sunlight, the R:FR ratio was about 1.1. However, it was reduced to 0.58 under the neutral filter (No 210). This shows that this filter failed to provide an appropriate control treatment. The effects of this filter were also variable, and mainly contributed to interactions between the light quality and species treatments.

The significant interactions between the R:FR ratio and the species treatments in RGR were due to the effects of the medium grey filter. When the effects of this filter were excluded, the responses of seedlings of both species showed the same pattern (Figure 5.2) suggesting that *C. africana* and *V. keniensis* are adapted to habitats with similar vegetational shadelight climate.

The increase in RGR with increasing R:FR ratio in both species was due to the effects of the NAR. Although the values of SLA (and LAR) were highest under reduced R:FR ratio in both species, these had no effects on the RGR. This was in contrast to the report of Kwesiga and Grace (1986) who found that under reduced R:FR ratio, the SLA enhanced the RGR of the light-demanding *T. ivorensis*.

The increase in the total dry weight with increasing R:FR ratio in seedlings of *C. africana* was consistent with previous results reported for *T. ivorensis* and *K. senegalensis* (Kwesiga and Grace, 1986) and for several temperate herbaceous plants (Corré, 1983b). The weak response in total dry weight by seedlings of *V. keniensis* to changes in R:FR ratio was unexpected, as this species seems to be light-demanding. The increase in height growth with increasing R:FR ratio in seedlings of *C. africana* was in contrast with the observations of Kwesiga and Grace (1986). These authors found increased height growth as a result of reduced R:FR ratio in seedlings of *T. ivorensis* and *K. senegalensis*. Warrington *et al* (1988) also observed larger height increments in plants grown under simulated canopy shade than in those grown under R:FR ratios simulating full daylight. In seedlings of *V. keniensis*, the slight differences in height growth among the seedlings grown under the different R:FR ratios seems to suggest that the height growth was enhanced under reduced R:FR ratio. This species seemed to display optimum height growth under R:FR ratio of 0.36 which can be considered as typical of shadelight in small to medium size forest gaps. Because seedlings of *V. keniensis* seemed unresponsive to an increase in R:FR ratio and PPFD in total dry weight and height growth, this suggests that this species may not be a strong light demander.

The increase in specific stem length in response to decrease in R:FR ratio in seedlings of both species supported the hypothesis that reduction in R:FR ratio results in marked stem extension. However, the absolute stem elongation was not observed especially in seedlings of *C. africana* growing under reduced R:FR ratio. This was possibly because of the very low R:FR ratio. In *Eucalyptus grandis*, an important plantation species in Kenya, Hoad and Leakey (in press) observed longer shoots in stockplants grown at low R:FR ratios (0.4 and 0.7) than in those grown at high (3.5 and 6.5) R:FR ratios. Warrington *et al* (1988) and Kamaluddin (1991) have observed increased stem extension in light-demanding species but did not observe such increases in shade-tolerant species. The specific stem length was greater in *V. keniensis* than in *C. africana* although the latter is more light-demanding. The hypothesis that *C. africana* displays greater stem extension was, therefore, not supported.

Reduction in R:FR ratio did not enhance internode length in seedlings of either species. This was in contrast to observations made on other species (Corré 1983b; Sasaki and Mori, 1981; Kamaluddin, 1991).

The increase in SLA with decreasing R:FR ratio in both species was in agreement with the results of Kwesiga and Grace (1986) on *T. ivorensis*. However, these authors did not find any significant effects of reduced R:FR ratio on seedlings of *K. senegalensis*. Other authors have also not found significant effects of reduced R:FR ratio on seedlings of several species (Morgan and Smith, 1981; Kamaluddin 1991).

Although the LWR and the SWR increased with the decrease in R:FR in both species, the main increase was in the SWR. This indicates that increased stem extension was associated with greater allocation of biomass to the main stem. Similar results have been reported for: *P. radiata* (Warrington *et al*, 1988), *A. chinensis* (Kamaluddin, 1991) and *E. grandis* (Hoad and Leakey, in press). The increased allocation of biomass to the stem and leaves was achieved at the expense of the roots. This was in agreement with the report of Sasaki and Mori (1981), but contrasted that of Kamaluddin (1991) who reported increased allocation of the dry matter to the stem at the expense of the development of the leaf area. The greater allocation of biomass to the stem in seedlings of *V. keniensis* indicates that the stem height was enhanced in this species under reduced R:FR ratio. The shift in biomass allocation from the roots to the shoot will increase the competitiveness of seedlings of *C. africana* and *V. keniensis* in presence of neighbouring plants.

5.3 EXPERIMENT 2: EFFECTS OF SUDDEN EXPOSURE OF SEEDLINGS TO FULL SUNLIGHT

5.3.1 MATERIALS AND METHODS

5.3.1.1 Treatments, Experimental Design and Plant Materials

This second experiment was a continuation of Experiment 1. The treatments, were therefore the same as those described in the first experiment. The experiment was started with 12 seedlings of each species which had been grown for 8 weeks under each of the 4 filter screen-houses. On the morning of the 15th June 1993, half of the seedlings of each species in each filter treatment were randomly selected for initial harvest. The remaining seedlings were then heavily watered and the screen-houses removed. The seedlings were also heavily watered in the evening of the same day. Subsequent waterings were carried out regularly as described in Chapter 2.

5.3.1.2 Measurement of Microclimate

Data on PPFD, temperature and VPD were collected for 10 consecutive days from 15th to 24th June 1993. The methods and procedures used were similar to those described in Chapter 2. However, only one quantum sensor and one psychrometric unit were used. Figure 5.8 shows the daily variation in PPFD, temperature and VPD during the 10 days of exposure of seedlings to the full sunlight.

When the seedlings were exposed to the full sunlight conditions, they experienced increases in R:FR ratio, irradiance and vapour pressure deficits, but decreases in temperature. The seedlings previously grown at very low R:FR ratio and low irradiance received 55-fold and 7-fold increases in R:FR ratio and PPFD respectively. For the seedlings grown under low and medium R:FR ratios and irradiance, the increases in PPFD and VPD levels were about two-fold while the temperature decreased by about 2.5 °C. The temperatures within the screen-houses

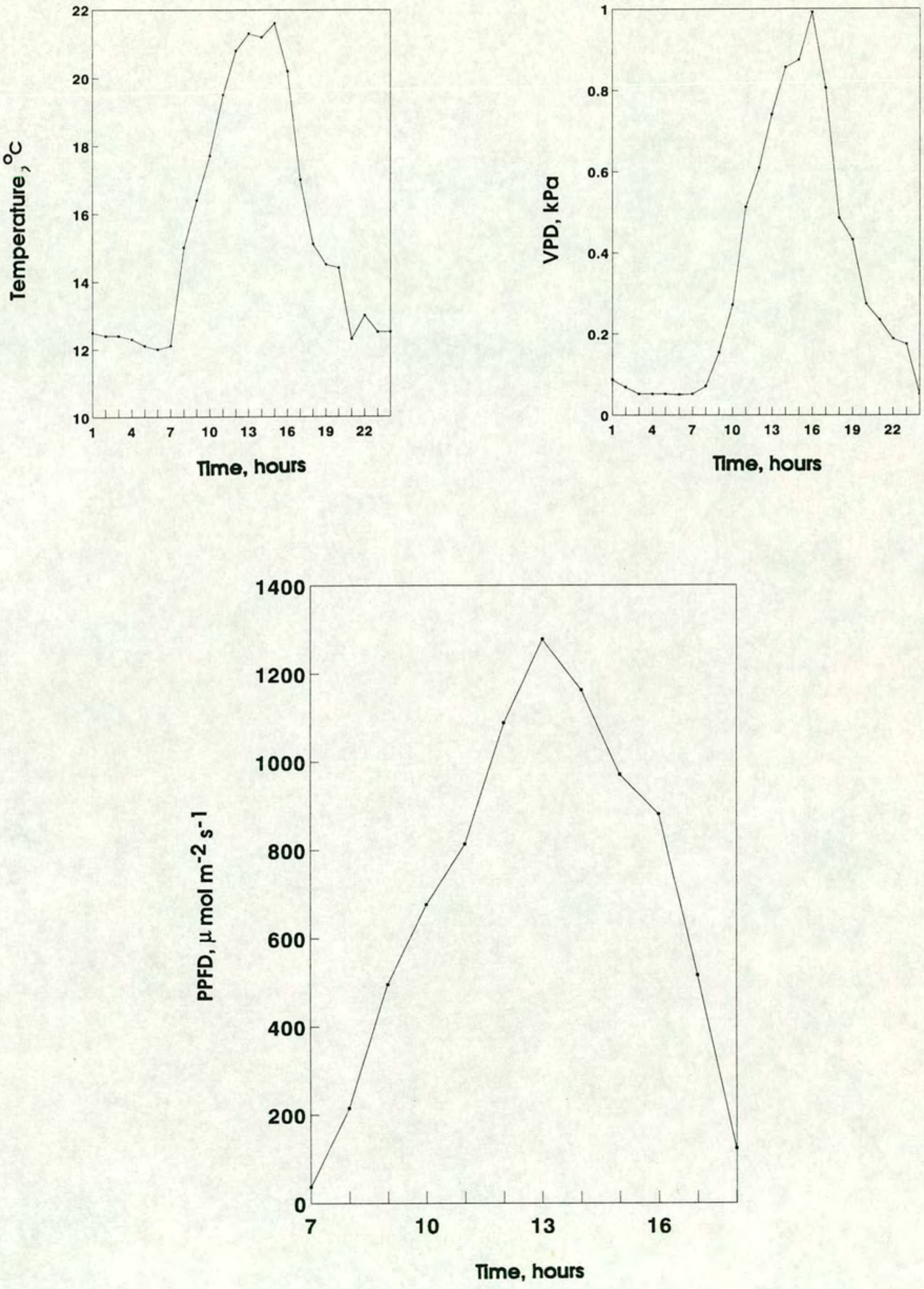

Figure 5.8. Variation in mean PPFD, temperature and VPD when the seedlings were exposed to full sun environment.

were higher probably due to inadequte ventilation, and also it seems the screen-houses acted like green houses.

5.3.1.3 Data Collection and Analysis

Two harvests were made in this experiment. The initial harvest was carried out at the start of the experiment and the second 5 weeks later. The sample size was 6 seedlings in the first harvest but varied from 2 to 5 seedlings in the second harvest. Visual observations on conditions of seedlings and the number of surviving leaves were assessed on a weekly basis. The harvesting methods and procedures used were similar to those described in section 5.2.1.5. The data were however, not derived on net assimilation rate and relative growth rate because of low survival in seedlings grown under very low R:FR ratio (under the dark green filter). Analysis of variance was carried out on assessed and derived parameters in the final harvest.

5.3.2 RESULTS

5.3.2.1 Leaf Changes

The effects of exposing seedlings to the full sun environment were evident in the afternoon of the day the experiment started. Leaf bleaching occurred in seedlings previously grown under the dark green filter No. 424 (R:FR ratio, 0.02; PPFD, 98.8 μ mol m^{-2} s^{-1}). By the second day of exposure, the bleaching was followed by severe scorching of some leaves resulting in some leaf mortality. However, during the first two days, no adverse effects were observed in seedlings previously grown under low and medium R:FR ratios.

As shown in Figure 5.9, the number of leaves generally decreased in the first week. Leaf losses were due to leaf mortality in seedlings previously grown under the dark green filter. In seedlings previously grown under moss green, pea green and medium grey filters, leaf losses were due to abscission. Under these three filter screens, light bleaching, scorching and wrinkling in some leaf laminae were observed in the second week. This was soon followed by production of new leaves leading to increase in their number by the second and third weeks. In seedlings of *V. keniensis* previously raised at low (0.02 and 0.36) R:FR ratios, the leaf number increased at the end of the fourth week. In those of *C. africana*, also previously grown at R:FR ratio of 0.02, leaf number increased during the same time (Figure 5.9). In the final harvest, the number of leaves was significantly affected by the previous R:FR ratio treatments

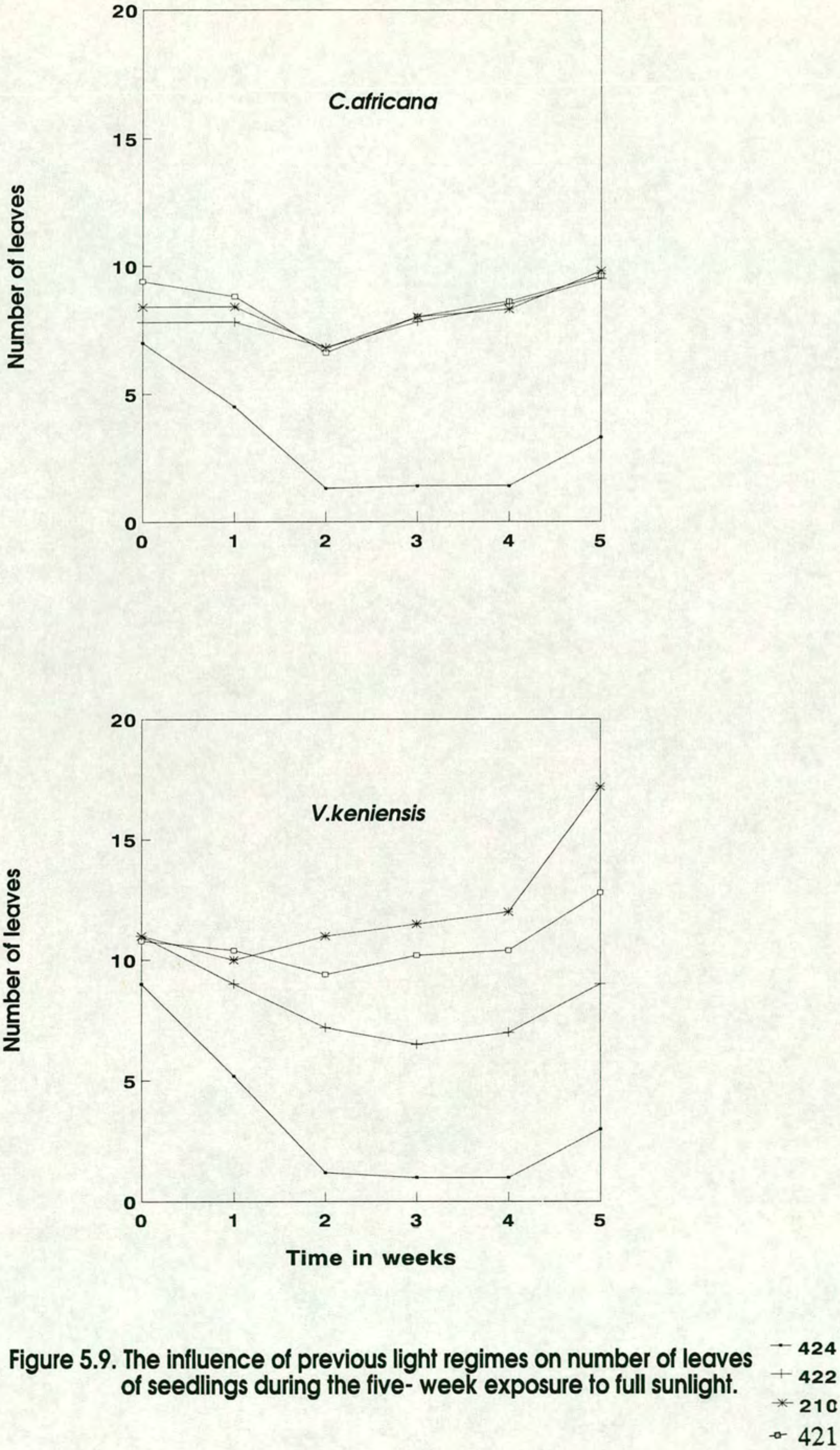

Figure 5.9. The influence of previous light regimes on number of leaves of seedlings during the five- week exposure to full sunlight.

(Table 5.5). Seedlings of *V. keniensis* had higher number of leaves than those of *C. africana*. Some seedlings of *V. keniensis* previously grown at medium (0.58) R:FR ratio produced side shoots which almost doubled the number of leaves in this treatment (Figure 5.9). At the end of the experiment the mortality of seedlings previously grown at very low R:FR ratio were 50% and 25% for *V. keniensis* and *C. africana* respectively. None of the seedlings in the other previous R:FR ratio treatments died as a result of exposure.

5.3.2.2 Height Growth

Growth in height is shown in Figure 5.10. In both species, height growth generally increased when the seedlings were exposed to the full sun. The previous R:FR ratio treatments had significant effects on height growth of seedlings (Table 5.5). Height growth was greatest for seedlings previously grown under pea green filter No. 421 (R:FR ratio of 0.65) and lowest for those previously grown at very low R:FR ratio. Seedlings of *C. africana* were significantly taller than those of *V. keniensis*. Seedlings of the latter previously grown under very low R:FR ratio showed little increase in height growth during the five-week period (Figure 5.10). Height growth was slightly depressed in seedlings of this species previously grown at medium (0.58) R:FR ratio and this resulted in significant interactions between the light quality and species treatments.

5.3.2.3 Total Dry Weight

There was a marked increase in total dry weight when the seedlings were exposed to the full sunlight (Figure 5.10). In both species, the total dry weight generally increased with increasing previous R:FR ratios. However, seedlings of both species grown previously at very low R:FR ratio showed no increase in dry weight (Figure 5.10). The previous R:FR ratios significantly affected the total dry weight in the final harvest (Table 5.5). Seedlings previously grown at medium R:FR ratio had the greatest total dry weight while those previously grown at very low R:FR ratio had the lowest. There were no significant differences in total dry weight between the seedlings previously grown at low (0.36) and medium (0.58 and 0.65) R:FR ratios. The increase in total dry weight was rapid more in seedlings of *C. africana* than in those of *V. keniensis*. The differences were significant.

Table 5.5: Summary of results on analysis of variance at the final harvest on the effects of exposing seedlings of *C. africana* and *V. keniensis* to full sunlight. The seedlings had been grown for 8 weeks at R:FR ratio regimes of 0.02, 0.36, 0.58 and 0.65.

Parameter	Treatments and interactions		
	R:FR ratio	Species	R:FR ratio x species
Total Dry Weight	****	****	**
Height growth	***	***	*
Number of leaves	***	*	ns
SLA	ns	ns	ns
LAR	ns	ns	ns
LWR	*	ns	*
SWR	****	ns	ns
RWR	ns	ns	ns

Symbols: ns = not significant at P<0.05;

* = significant at P<0.05;

** = significant at P<0.0l;

*** = significant at P<0.001; and

**** = significant at P<0.0001.

5.3.2.4 Morphological Changes

There were decreases in specific leaf area (SLA) and LAR when the seedlings were exposed to the full light (Figure 5.11). The two parameters showed the same patterns in their response and were not significantly affected by the R:FR ratios (Table 5.5). At the end of the experiment, seedlings of *C. africana*, previously grown under the four R:FR ratios had almost the same SLA. However, in seedlings of *V. keniensis* previously at very low R:FR ratio, the SLA decreased slightly. The LAR in seedlings of both species was also reduced on exposure to full sunlight (Figure 5.11). It was not affected by the previous R:FR ratio treatments and it did not differ between the two species.

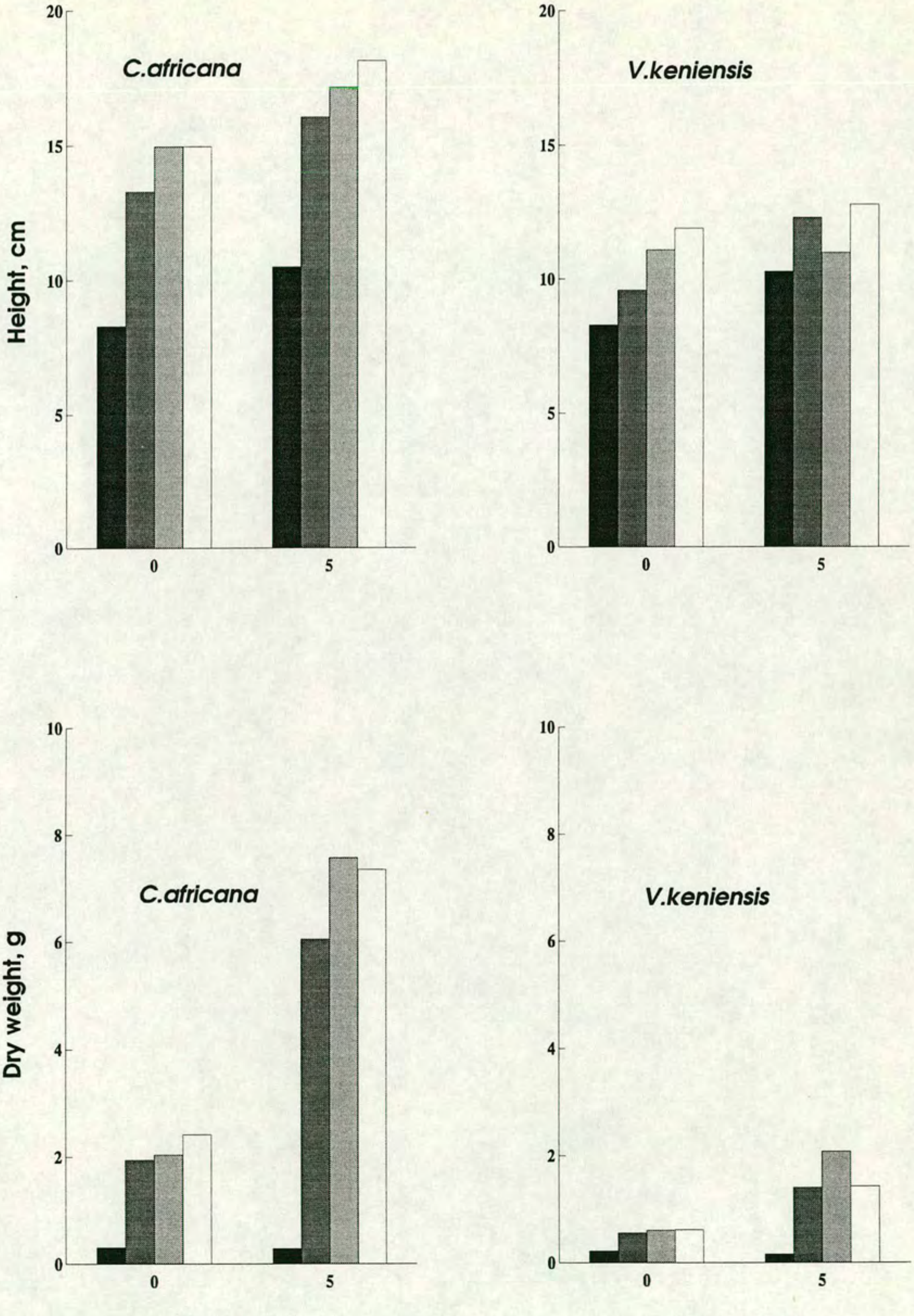

Figure 5.10. Changes in height growth (top) and dry weight (bottom) in seedlings previously grown under different R:FR ratios and exposed to full sunlight for five weeks.

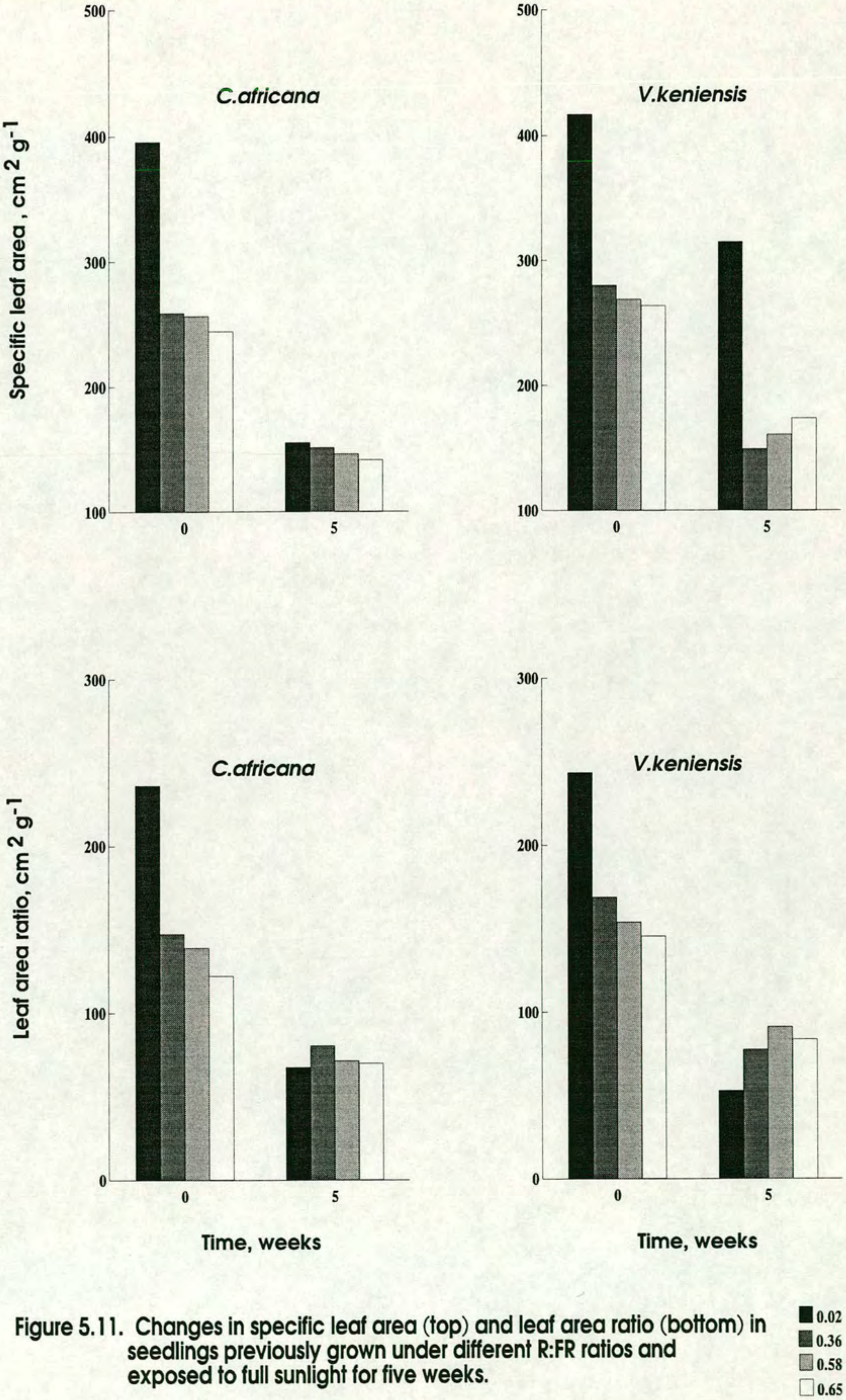

Figure 5.11. Changes in specific leaf area (top) and leaf area ratio (bottom) in seedlings previously grown under different R:FR ratios and exposed to full sunlight for five weeks.

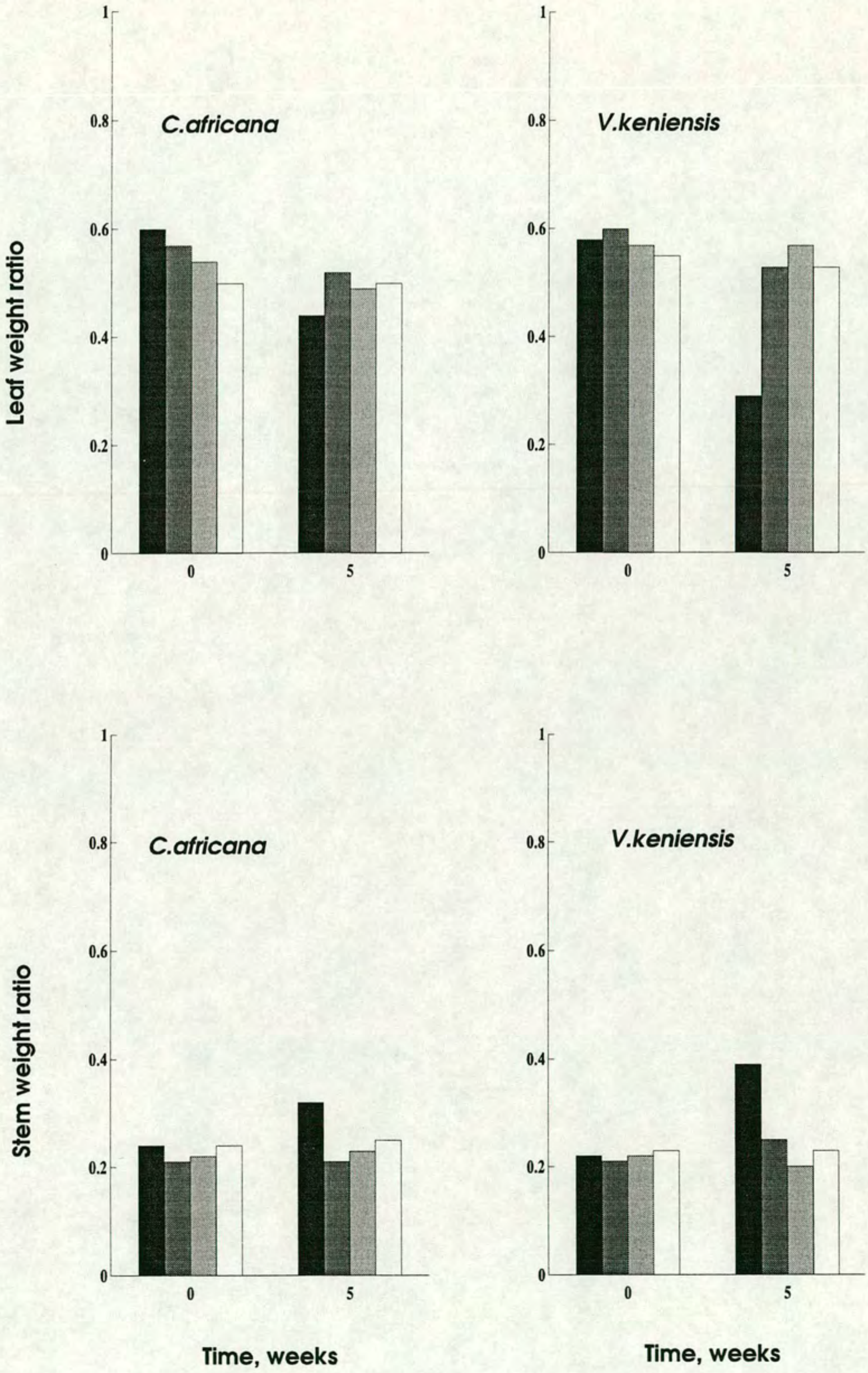

Figure 5.12. Changes in leaf weight ratio (top) and stem weight ratio (bottom) in seedlings previously grown at different R:FR ratios and exposed to full sunlight for five weeks.

5.3.2.5 Biomass Distribution

When the seedlings were exposed to the full sunlight for 5 weeks, the distribution of biomass generally differed from that at the start of the experiment (Figures 5.12). The leaf weight ratio (LWR) decreased in seedlings previously grown under light regime with reduced R:FR (Figure 5.12). It was significantly affected by the previous R:FR ratio treatments but did not differ between the species. Seedlings grown previously at low and medium R:FR ratio displayed the greatest LWR while those previously grown under very low R:FR ratio had the lowest, especially those of *V. keniensis.*

The stem weight ratio (SWR) increased when seedlings were exposed to the full sunlight during the 5-week period (Figure 5.12) and the response was opposite to that of the LWR. The effects of the previous R:FR ratio on SWR were significant and much stronger than their effects on LWR. Seedlings previously raised under very low R:FR ratio had the greatest SWR while those previously grown at medium R:FR ratio had the lowest.

The RWR ratio was generally unaffected by exposure of seedlings to the full sunlight. It tended to increase in seedlings of both species previously grown under very low R:FR ratio. The previous R:FR ratio treatments had no significant effects on the RWR.

5.3.3 DISCUSSION

Before the seedlings were exposed to the full sunlight, they had been generally grown under simulated low and moderate vegetational shadelight regimes for 4 weeks. Low light regime was obtained under the dark green filter and simulated shadelight a under small forest gap with an irradiance of 12% of full sunlight. The light regime under moss green, pea green and medium grey filters was moderate and simulated conditions under medium size to large forest gap with irradiance varying from 28% to 38% of full sunlight.

Sudden exposure of seedlings of both species to the full sunlight resulted in some damage as indicated by the mortality of the leaves and seedlings. It seems the full sun environment was too desiccating for seedlings with thin leaves (high SLA). Seedlings previously grown under moderate light regimes with thicker leaves (lower

SLA) were slightly damaged as shown by the light scorching. Seedlings of *V. keniensis* seem to be more susceptible to mortality from exposure to full sun than those of *C. africana*. Bleaching, scorching and wrinkling of leaf laminae observed in the present experiment were similar to earlier observations in this study (see Chapter 4). The transfer of seedlings from shade to full sunlight produced similar effects of leaf bleaching, scorching and leaf mortality in seedlings of *Shorea macroptera* but not in *Trema tomentosa* although both species are light -demanding (Turner and Newton, l990). Leaf bleaching and/or scorching have also been reported in seedlings of some tropical trees transferred from shade to full sunlight or high irradiance (Oberbauer and Strain, 1985; Kigomo, 1989; Kamaluddin and Grace, 1992a).

The increase in the number of leaves indicated that the seedlings had recovered and had probably acclimated to the full sun environment. Seedling recovery seems to have been related to the previous light regimes. It was slower in seedlings previously grown under low light regime and generally faster for those previously grown under moderate light regimes.

Since there were almost no increases in height and total dry weight in seedlings of both species previously grown under low light regime when exposed to the full sun environment, this suggests that the RGR was negative. It also suggests that these seedlings had not fully acclimated to the new environment five weeks after exposure. High leaf losses seem to have contributed to the decline in growth. On exposure to the full sunlight, seedlings of *C. africana* previously grown under moderate light regime exhibited characteristics of a pioneer species due to rapid growth in height and large increases in biomass production. Although the height growth and dry weight increased also when seedlings of *V. keniensis* previously grown under moderate light regime were exposed, the increases were moderate and tended to decline with increasing irradiance. This confirms earlier observations that this species may not be a strong light demander (see section 5.2.3). The production of side shoots with smaller leaves in some of the seedlings previously grown under the moderate light regime suggests that the terminal shoots were either damaged or had stopped growing. This seems to have resulted in depressed height increment by main stem, due to competition from the laterals in some of these seedlings. Kamaluddin and Grace (1992a) have reported production of side shoots by seedlings of a pioneer species *B. javanica* which were transferred from shade to high irradiance. Fetcher *et al* (1983) also reported a reduced height increment in seedlings of another pioneer species, *H. appendiculatus* transferred from full shade to full sunlight.

Decreases in SLA when seedlings were exposed to the full sun environment show that the new leaves had become thicker, as observed earlier in this study (see Chapter 4). Leaf thickening (decrease in SLA) in seedlings exposed to full sun environment is an adaption to reduce water losses and also minimise injury under high irradiance. In seedlings of *V. keniensis* previously grown under low light regime, the mean data was based on two seedlings as the others died. This gave unreliable results due to inadequate replication.

The decrease in LAR was due to the decrease in SLA. For seedlings previously grown under low light regime, however, it seems that high leaf losses also contributed to reduction in the LAR. In seedlings previously grown under moderate light regime, it also appears that the new leaves produced were smaller and this reduced the LAR. This is because the number of leaves at the start and at the end of the experiment were about the same and were even higher in seedlings of *V. keniensis*. These results are in contrast to those reported by Kamaluddin and Grace (1993) who found increased LAR in seedlings of *B. javanica* transferred from low light to high light. These authors did not, however, observe any leaf shedding in their seedlings transferred to high light. The decreases in SLA and LAR in this experiment were similar to those reported for seedlings of *Cordia megalantha* transferred from full shade to large gap (Bongers *et al*, 1988).

When the seedlings were exposed to full sunlight, the LWR decreased in those previously grown under low light regime. This decrease was due to high leaf losses. Under the same light regime, the increases in SWR and RWR did not seem to be a result of increased allocation of biomass to stem and roots but rather to the loss of leaves.

Although the exposure of seedlings to full sunlight was sudden in this experiment, the damage was only severe in those previously grown at very low (0.02) R:FR ratio and low (12% of full sun) irradiance. Seedlings previously grown at medium (0.36 to 0.65) R:FR ratios and about medium (28 to 38% of full sun) irradiance, were less affected. These results suggest that had the exposure been more gradual, seedling mortality would not have probably occurred in those previously grown at very low R:FR ratio. In the same seedlings, leaf losses would have been less. Growth would have probably also increased slightly. In seedlings previously grown at medium R:FR ratios acclimation and growth would have probably been more rapid. Being a more light demanding species, seedlings of *C. africana* would have probably acclimated faster than those of *V. keniensis.*

5.4 CONCLUSIONS

The interpretation of the results of the first experinment was complicated by the fact that the R:FR ratio and irradiance treatments were confounded. However, since a decrease in irradiance is usually accompanied by a decrease in R:FR ratio, the results suggest that seedlings of *C. africana* and *V. keniensis* are unlikely to display extreme stem extension under vegetational shadelight with low to medium R:FR ratios, for example under medium size and large forest gaps. In deep shade with very low R:FR ratio, seedlings of both species will show some marked stem extension and will shift biomass partitioning from roots to stems. Being light demanding, however, seedlings of these species will rarely be found under such understorey forest habitats. Seedlings of *V. keniensis* showed greater stem extension than those of *C. africana* although the latter is more light-demanding. This seems to suggest that the response to light quality may not be related to the species` light requirements or its ecological distribution but may be species-specific.

The second experiment has shown that the previous light regimes are likely to influence the responses of seedlings of both species when exposed to full sunlight environment. Seedlings growing in dense shade with an irradiance of 12% of full sunlight or lower are likely to be adversely affected by sudden formation of a large gap or clearing over them. The sudden increase in irradiance will result in reduced survival and growth. Seedlings of *V. keniensis* will be more adversely affected than those of *C. africana.* However, seedlings of both species growing under moderate shade with irradiances of 28 - 38% of full sun will survive well and their growth enhanced following formation of a larger gap or clearing over them. Seedlings of *C. africana* show more rapid positive response than those of *V. keniensis*.

The two experiments suggest that seedlings of *V. keniensis* are moderately light-demanding and are likely to show optimum growth under moderately shaded environment.

CHAPTER 6

GROWTH RESPONSES OF TREE SEEDLINGS TO VARYING SHADE LEVELS IN A FOREST CLEARING

6.1 INTRODUCTION

In Kenya, many areas of natural forests have been heavily disturbed through selective logging and clearing. The degraded areas vary in size from scattered canopy gaps to large abandoned clearings. These areas need to be rehabilitated for both protective and productive purposes. There is a growing interest in rehabilitating the damaged areas by planting indigenous tree species. However, there is inadequate understanding of their ecological requirements and there is also little experience on silvicultural management of these species.

Canopy gaps and clearings are characterized by increased irradiance, temperature and vapour pressure deficits (Burton and Mueller-Dombois, 1984; Fetcher *et al*, 1985; Eamus *et al*, 1990). Such areas are also rapidly invaded by weedy species which may retard regeneration. In Kenya, the most common among these colonisers are *Macaranga kilimandscharica, Neoboutonia macrocalyx, Trema guineensis, Piper capense* and *Vernonia auriculifera.*

Tree species differ in their requirements for light (Richards, 1952; Whitmore, 1985) and respond differently to environmental conditions associated with canopy gaps of different sizes (Denslow 1980; Popma and Bongers, 1988). Pioneer species show enhanced capacity to utilize high irradiance in gaps and clearings (Bazzaz and Picket, 1980). These species are highly amenable to silvicultural management (Turner and Newton, 1990) and can help in recovery of forest structure after disturbance (Bazzaz, 1991).

Few studies have been conducted under field conditions to determine the responses of seedlings of tropical tree species to the different levels of light associated with large canopy gaps and clearings (Nicholson, 1960; Fetcher *et al*, 1983; Popma and Bongers, 1988; Thompson *et al*, 1988; Eamus *et al*, 1990).

Nicholson (1960) compared the light requirements of seedlings of five species of the Dipterocapaceae grown under artificial shade frames in a forest clearing. He found that all species responded positively to some shading, at least in early stages of their growth. Fetcher *et al* (1983) studied the effects of full sunlight, partial shade (80% of full sunlight) and full (98%) shade on growth and morphology of seedlings of a pioneer species *Heliocarpus appendiculatus* and a shade-tolerant species *Dipteryx panamensis*. They found that growth in height increased in *H. appendiculatus* in response to full shade and decreased under full sunlight. However, height growth was unaffected by irradiance in *D. panamensis*. In contrast, biomass of *H. appendiculatus*, was not significantly greater in full sunlight than in partial shade, whereas it was for *D. panamensis*. In a related study, Popma and Bongers (1988) studied the responses of seedlings of ten forest trees to four levels of irradiance in: a forest understorey, a small gap (with an area of about 200 m^2) and a large gap (500 m^2). They found that although the growth was enhanced in gaps, the effects were stronger in the large gap. However, some species displayed high growth rates under both shade and sun conditions. Thompson *et al* (1988) made observations on persistence and comparative growth of seedlings of several Australian species within disturbance gaps. They found that *Flindersia brayleyana* displayed broad tolerance to irradiance under small, medium and wide gaps of a mature forest. In a more recent study, Eamus *et al* (1990) compared the response of seedlings of *Terminalia ivorensis* to irradiance under four different site treatments: undisturbed forest, light clearing done manually, partial clearing done mechanically and complete clearing. Growth was greatest under partial clearing done mechanically and least under the manual treatment. High initial mortality was observed on the site which was completely cleared but the seedlings later grew rapidly.

The above studies indicate that seedlings of tropical tree species respond differently to large gaps and clearings. Adequate information on silvicultural requirements of individual species is, therefore, necessary for any success in reforestation programmes in heavily disturbed areas. The aim of the present experiment was to determine the responses of seedlings of four species to different levels of light. The species were *C.africana*, *V.kenienisis*, *M.lutea* and *O.capensis*. These species are important for various tree planting activities in Kenya (see Chapter 2). The hypothesis was that the four species will show similar responses to different irradiance levels and that they will grow faster under full sunlight.

Seedlings of the four species were grown under four levels of irradiance in a forest clearing. The irradiance treatments were obtained by use of 3 timber frames with different light interception which provided dense, moderate and light shade. The effects of these levels of shade on growth of seedlings were compared to that of the full sunlight treatment. Timber frames of this sort do not usually affect the light quality, but there might be a slight reduction in R:FR ratio under very low irradiance.

6.2 MATERIALS AND METHODS

6.2.1 Experimental Area

The experiment was located in a clearing covering 0.8 ha in Chuka Forest Reserve, on the eastern side of Mt. Kenya. The site had a moderate south east facing slope and it was 0.5 km north of Chuka Forest Station. The location and site characteristics of the area are described in Section 2.1. The clearing was made in 1985 for the establishment of a tea (*Camellia sinensis*) nursery. In 1988, the nursery was abandoned and the site was colonized mainly by grasses and a few pioneering shrubs. The main grass species was *Pennisetum clandestinum* which was frequently cut and carried for stall-feeding of animals.

6.2.2 Treatments, Experimental Design and Layout

This was a split-plot experiment with 4 levels of light (three shade levels and full sunlight) as main treatments. The sub-treatments were seedlings of 4 species (*C. africana*, *V. keniensis*, *Olea capensis*, and *Markhamia lutea*). A randomized-block design of three replications was used. The light treatments were randomized within the blocks while the species were randomized within the light treatments.

The whole experiment occupied an area of approximately 0.20 ha. The blocks and main plots were laid out along the slope to minimize the effects of site variability. A distance of 5.0 m separated the blocks. The main plots were also 5.0 m apart. Twelve seedlings were planted in each sub-plot in 2 x 6 arrangement and at a square spacing of 1.0 m.

6.2.3 Plant Material

The experimental seedlings were raised in the Kenya Forestry Research Institute Nursery, Muguga. Seedlings of three species (*C. africana*, *V. keniensis* and *M. lutea*) were raised from seeds germinated in the nursery while those of *O. capensis* were from naturally germinated seedlings. Seeds of *C. africana* (Batch No. 139025/92) were collected from Kabete Farm, University of Nairobi. Those of *V. keniensis* and *M. lutea* originated from Mt. Kenya area (Meru Forest station and Kibirigwi Irrigation Scheme respectively).

In March 1992, the seeds of *C. africana*, *V. keniensis* and *M. lutea* were sown in a nursery seed bed with sand as germination medium. After seven weeks, germinated seedlings were transplanted into 20 cm-long (diameter 6.5 cm) polyethlene pots perforated at the bottom. The pots were filled with forest top soil, cow manure and gravel mixed in a ratio of 5:2:1 by volume respectively. At the time of transplanting, the seedlings of *C. africana*, *V. keniensis* and *M. lutea* averaged 2.0, 3.0 and 5.0 cm in height respectively. In June 1992, naturally germinated seedlings of *O. capensis* were collected from Kobujoi Forest Reserve in Western Kenya and transplanted into pots having similar size and potting mixture as those used for seedlings of the other three species. These seedlings were 4 to 6 months old and averaged 9.0 cm in height.

The seedlings of the four species were raised under the full sunlight conditions. They were watered and protected from insect damage as described in Section 2.3.1. In July 1992, they were top-dressed with NPK (20:10:10) fertilizer at the rate of 1.5g per seedling. In early October 1992, the seedlings were transferred from Muguga to Chuka Forest Station where they were also raised under full sunlight conditions. Some seedlings of *C. africana* had shed some of their leaves at the time of planting three weeks later.

6.2.4 Site preparation, Planting and Tending

Site preparation was done during the dry season in September 1992. Shrubs were cleared within the demarkated experimental area and 10 m away from the main plots. Grass and herbaceous vegetation were completely cleared by hoeing in the main plots. This was done to reduce weed competition after planting. Planting pits (20 cm in diameter and 25 cm in depth) were also dug during the dry season.

Planting was carried out on 29th and 30th October, 1992 after a week of heavy rains. During planting the largest seedlings of each species were selected and randomly assigned to the irradiance treatments. At the time of planting, seedlings of *M. lutea* and *O. capensis* averaged 13.0 cm in height while those of *C. africana* and *V. keniensis* were about 20.0 cm tall. The initial survival was good and dead seedlings were replaced within a week. The plots were maintained under weed free conditions up to the end of the experiment.

6.2.5 Light Treatments and Microclimate

The shade levels were obtained by use of artificial shade houses made with timber slats which were 50 mm wide and 12.5 mm thick. Each shade house (Plates 6.1 and 6.2) was 13.0 m long, 5.0 m wide and 2.0 m high. The 50 mm - wide slats were spaced as follows to provide the level of shade required: one slat per 67 mm (about 17 mm gap) for dense shade; one slat per 100 mm (50 mm gap) for moderate shade and one slat per 200 mm (150 mm gap) for the light shade. Construction of the shade houses started on 27th January, 1993 and was completed on 5th February, 1993. This was about three months after the planting. The shade houses could not be immediately constructed because funds were not available to buy the timber.

Measurements of PPFD, temperature and humidity were made for 7 days from 24th - 30th April 1993 and also for another 6 days from 7th - 12th July 1993 to characterize the microclimate within the irradiance treatments. The instruments and procedures used were the same as those described in Section 2.3.2. Sensors were placed at the centre of the main plots at a height of 20 cm above the seedlings. Because of an inadequate number of sensors, measurement of the microclimatic factors was not carried out in all the light treatments. Light quality was measured for four days at about noon (local time) using two hand-held red/far-red sensors described in Section 4.2.3. Twenty pair of readings were made in each treatment. Rainfall was recorded at Chuka Forest Station for the duration of the experiment.

Figure 6.1 shows the daily variation in PPFD and temperature within the light treatments. Daily PPFD values (mean and total) and the mean temperature are given in Table 6.1. Because of the more cloudy conditions in July, the irradiance received under each light treatment was about half of that received in April. The average irradiance for April and July as percentage of that under the full sunlight condition of the clearing were: dense shade 16%; moderate shade, 37% and light shade, 61%.

The absolute PPFD values under the treatments in this experiment were generally about 30% lower than those recorded in Chapter 3, but were close to those recorded in Chapter 4 (except under the full sunlight condition).

A gap created by a fallen tree in a tropical forest covers an area of about 400 m^2 (Poore, 1968; Whitmore, 1985) and the total daily PPFD received at the centre of such a medium size gap in a lowland tropical forest in Costa Rica ranged from 3.86 to 13.7 mol $m^{-2}d^{-1}$ (Fetcher et al, 1983; Chazdon and Fetcher, 1984 a & b). The irradiance levels of 4.8 and 10.9 mol $m^{-2}d^{-1}$ received under the dense and moderate shade in the present study, therefore, simulated light condition in a medium size gap. The irradiance levels received under the light shade and the full sunlight conditions in the clearing in the present study were within the range of those reported in clearings of 0.5 ha (Fetcher *et al*, 1983; Chazdon and Fetcher, 1984 a & b; Popma and Bongers, 1991) and in 1.0 ha clearing in Cameroun (Eamus *et al*, 1990). The quality of light under the four light treatments was almost the same. The slight reduction in R:FR ratio under the dense shade treatment was possibly due to reduced irradiance.

Temperature differences between the treatments were generally small especially for the month of April, which was the rainy season (Figures 6.1 and 6.2). The mean daily temperatures were lowest under the dense shade and highest under the full sunlight. In April the night temperatures tended to be higher under the dense shade than in other light treatments. The temperatures were about 3 °C lower in July than in April and this was possibly due to lower irradiance.

As shown in Table 6.1 and figure 6.2, the daily mean VPD was highest under the full sunlight treatment and lowest under the dense shade. Although April was wet while July was dry, the VPD was lower in the latter. This was because of the usually cold, cloudy and misty conditions in June to August in this area. There were larger differences in VPD between the shaded treatments in April than in July. The rainfall recorded in January was unusually high. However, average rainfall was received in the other months. June to September is usually dry in this area (Section 2.1).

Plate 6.1: **Timber shade-houses soon after constrution in the clearing. Seedlings under the shade-house shown on the front side received light level of 61% of full sunlight.**

Plate 6.2: **Seedlings under one of the shade-houses a few months before the final harvest. The tallest plants are of *V.keniensis*.**

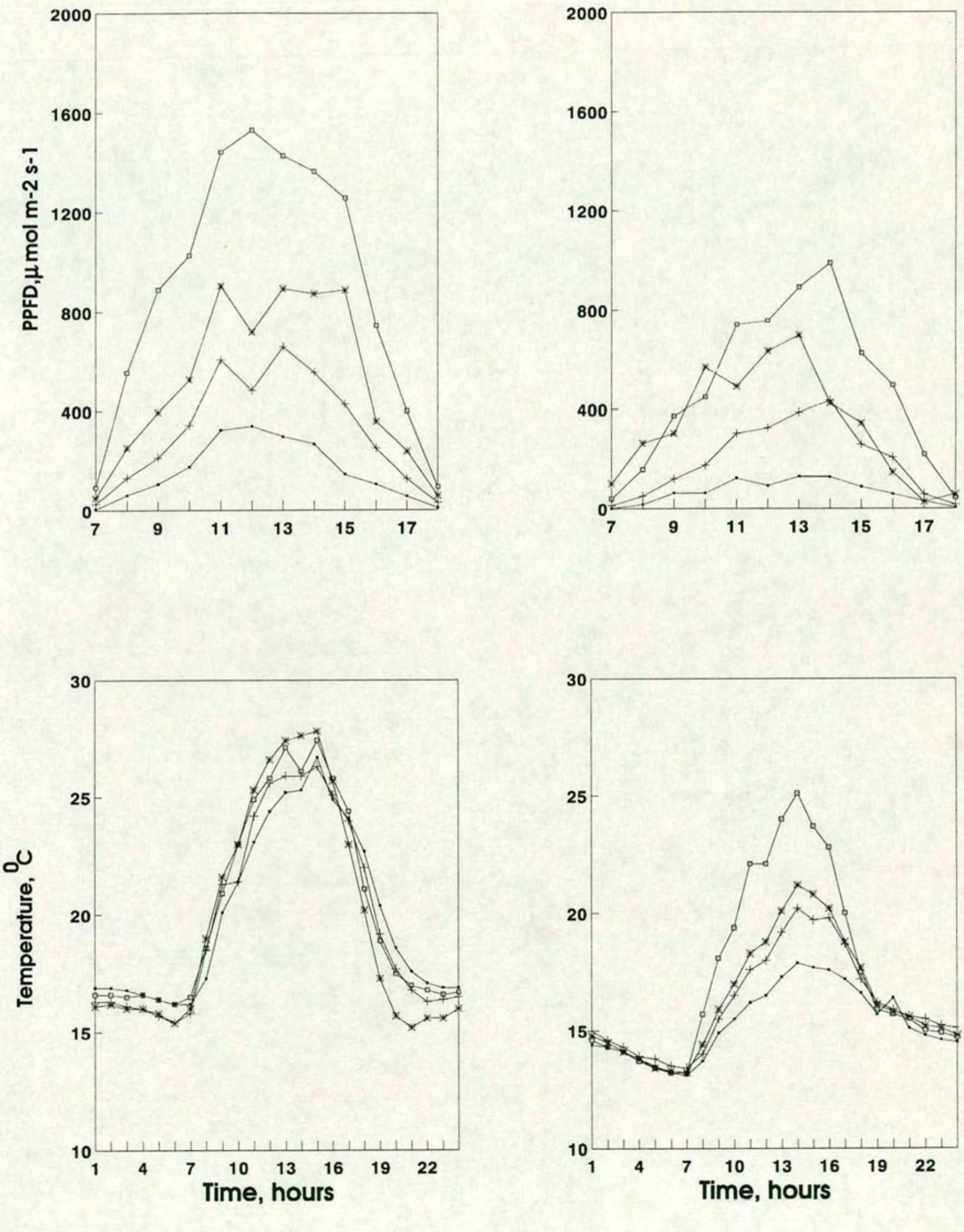

Figure 6.1 Mean daily variation in PPFD (top) and temperature (bottom) under different light levels in April (left) and in July (right) 1993.

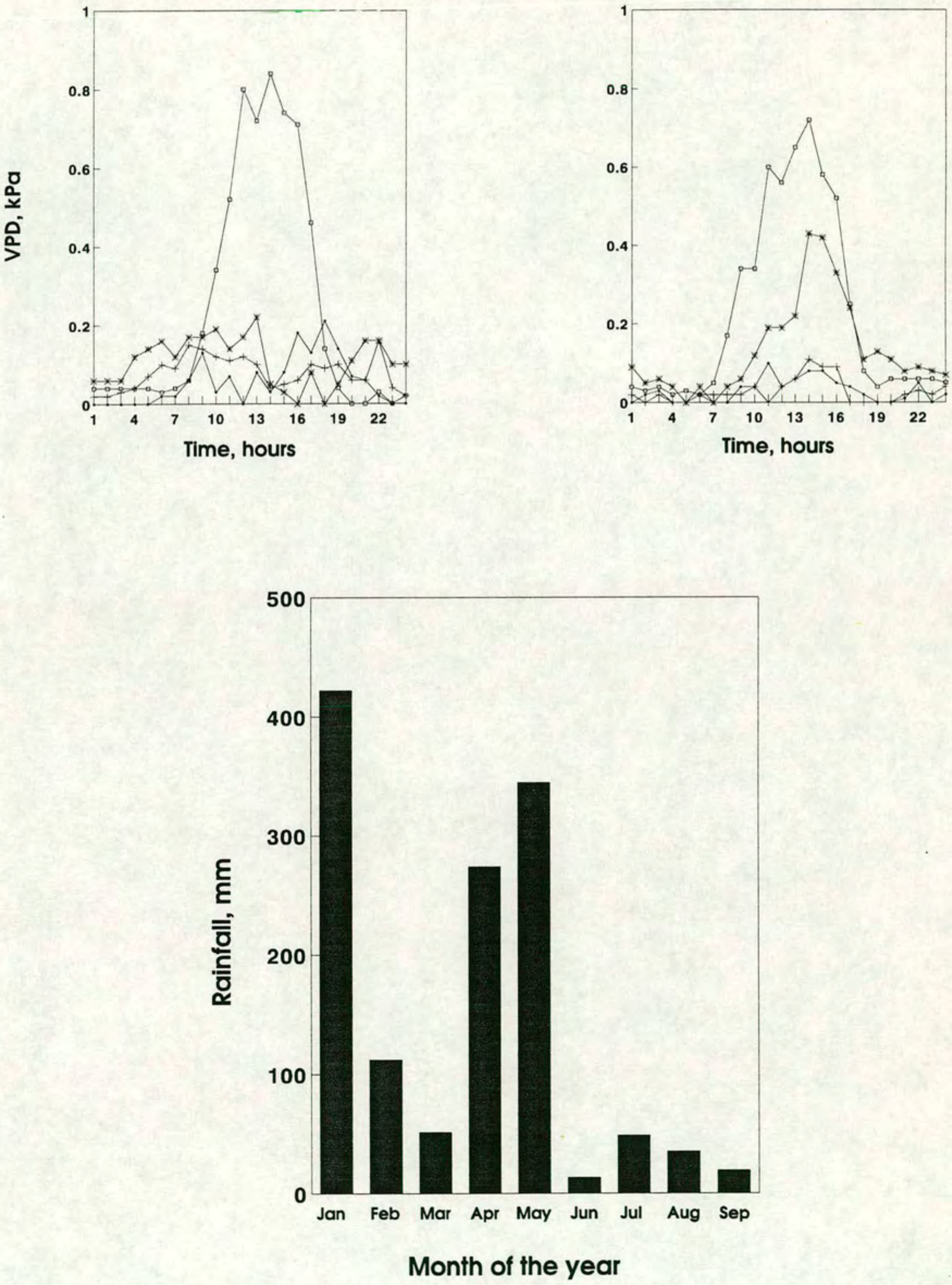

Figure 6.2 Top is mean daily variation in VPD under different light levels for April (left) and July (right) 1993. Bottom is monthly rainfall at Chuka Forest Station in 1993.

16%
37%
61%
100%

Table 6.1: Summary of PPFD, R:FR ratio, temperature and VPD under the four light treatments during the 7 days in April and 6 days in July 1993

Microclimatic factor		Irradiance treatments			
		Dense shade	Moderate shade	Light shade	Full sunlight
Mean PPFD (April), μmol m^{-2} s^{-1}		157.2	320.1	512.7	901.3
Mean PPFD (July), μmol m^{-2} s^{-1}		67.1	195.8	336.2	482.9
Average for April and July	Mean daily, μmol m^{-2} s^{-1}	112.2	258.0	424.4	692.1
	Total daily, mol m^{-2} d^{-1}	4.8	10.9	18.3	29.9
	% full sunlight	16	37	61	100
R:FR ratio		0.88	1.07	1.04	1.10
Mean daily temperature (April), °C		19.0	19.9	19.8	20.2
Mean daily temperature (July), °C		15.3	16.2	16.4	17.4
Mean daily VPD (April), kPa		0.06	0.07	0.11	0.24
Mean daily VPD (July), kPa		0.03	0.03	0.13	0.22

6.2.6 Data Collection

Seedlings were assessed at the ages in weeks (and months) of 0 (0), 2 (0.5), 6 (1.5), 11 (2.7), 15 (3.8), 21 (5.1) and 35 (8.7) from the commencement of the experiment. At each assessment, the height of the seedlings was measured and the number of surviving leaves counted. The crown width (diameter) and number of primary branches were also assessed up to the age of 5.1 months. The crown width was measured in two opposite directions and the means calculated. Two harvests were made on 23rd - 26th April and on 22nd - 24th October 1993 at the ages of 2.7 and 8.7 months respectively. Within about three months from the start of the experiment (six months from planting), the canopies were closing in some sub-plots of seedlings of *C. africana* and *V. keniensis*. The first harvest was therefore made to reduce mutual shading of seedlings. In this first harvest, half the individuals of each sub-plot were harvested by excavating alternate seedlings. Excavated roots were washed. Fallen leaves were also collected. The roots, stem and leaves were not kept separately. Harvested samples in each sub-plot were kept together and partially dried in the sun at Chuka Forest Station before transporting to KEFRI Headquarters for oven-drying and dry weight determination. In both harvests, drying took several weeks because there were no adequate number of ovens.. Samples not immediately dried were spread over the benches in the laboratory and turned over repeatedly to avoid decomposing. The samples were oven-dried to constant weight. Analysis of variance was carried out on height increment (between the initial and final measurements), dry weights, number of surviving leaves, number of primary branches and mean crown width.

6.3 RESULTS

A Summary of results on the analysis of variance is given in Table 6.2. Table 6.3 also shows the means and standard errors for the parameters assessed.

6.3.1 Height Growth

Height increment was significantly affected by the irradiance treatments (Table 6.2). For all species except *C. africana*, height growth was greater in shaded treatments than under full sunlight conditions of the clearing (Figure 6.3). In *V.keniensis* and *M. lutea*, seedlings grown under the dense shade showed greatest height growth. In *O. capensis* the greatest height growth was shown by seedlings grown under the moderate shade. The poorest height growth in these three species was shown by seedlings grown under the full sunlight. In contrast, seedlings of *C. africana* displayed the best height growth under full sunlight. At the start of the experiment and later on, seedlings of *M.lutea* growing under full sunlight were browsed by grasshoppers and the damaged seedlings recovered slowly.

Height growth of *V. keniensis* was faster than that of the other species. Five months after the start of the experiment, some seedlings of *V. keniensis* had grown up to the top of the shade houses. Most of these seedlings were under the dense shade treatment. While height growth continued in shaded seedlings after the fifth month, it slowed down in seedlings grown under the full sunlight treatment. As a result, shaded seedlings of this species were 50 to 100 cm taller than those grown in the open (Figure 6.3).

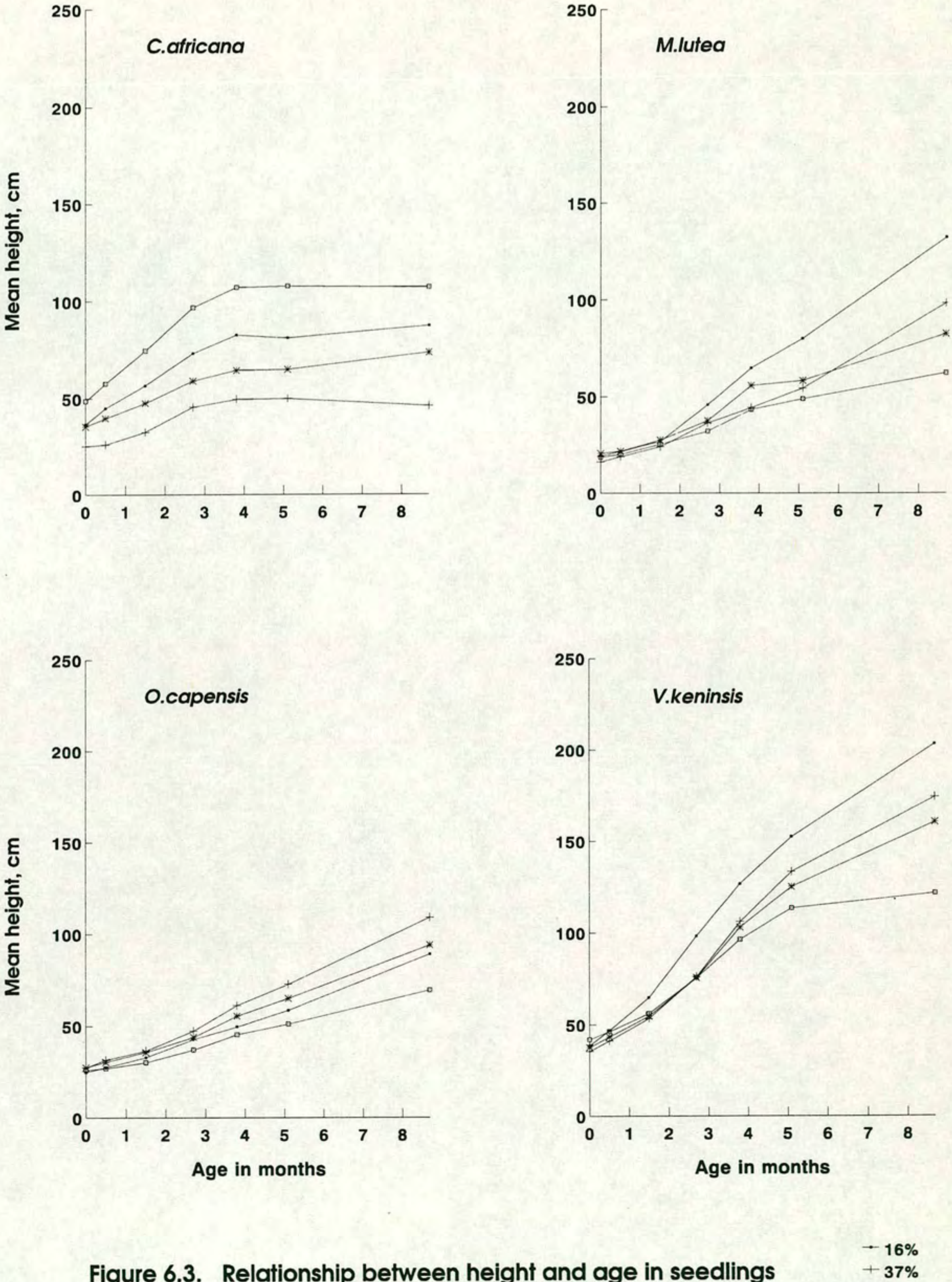

Figure 6.3. Relationship between height and age in seedlings grown under different irradiance levels.

In seedlings of *C. africana* initial differences in height growth was due to site differences. Significant interactions were observed between the irradiance and species treatments. This was a result of a different response shown by *C. africana* compared to the other species. After the fourth month, there was no increase in height growth in seedlings of this species regardless of the irradiance treatment (Figure 6.3).

6.3.2 Dry Weight

Table 6.2 shows that the dry weight was significantly affected by the irradiance treatments at initial harvest at 2.7 months but not in the final harvest at 8.7 months. The differences between the species were significant in both harvests. The interactions were stronger in the first harvest than in the final harvest.

By the first harvest, the irradiance treatments had not shown any effects on dry weight of seedlings of *M. lutea* and *O. capensis* (Figure 6.4). On the other hand, the dry weight generally increased with increasing irradiance in seedlings of *C. africana* and *V. keniensis*.

Table 6.2: The effects of irradiance treatments on growth, leaf number, number of primary branches and crown diameter of seedlings of *C. africana*, *V. keniensis*, *M. lutea* and *O. capensis*.

Parameter	Light	Species	Light x species
Height increment	*	****	*
Total dry weight at 2.7 months	**	****	****
Total dry weight at 8.7 months	ns	****	*
Leaf number at 8.7 months	ns	****	ns
No. of primary branches at 5.1 months	**	****	*
Crown diameter at 5.1 months	ns	****	**

Symbols: ns = not significant at $P<0.05$;
* = Significant at $P<0.05$;
** = Significant at $P<0.01$;
*** = Significant at $P<0.001$ and
**** = Significant at $P<0.0001$

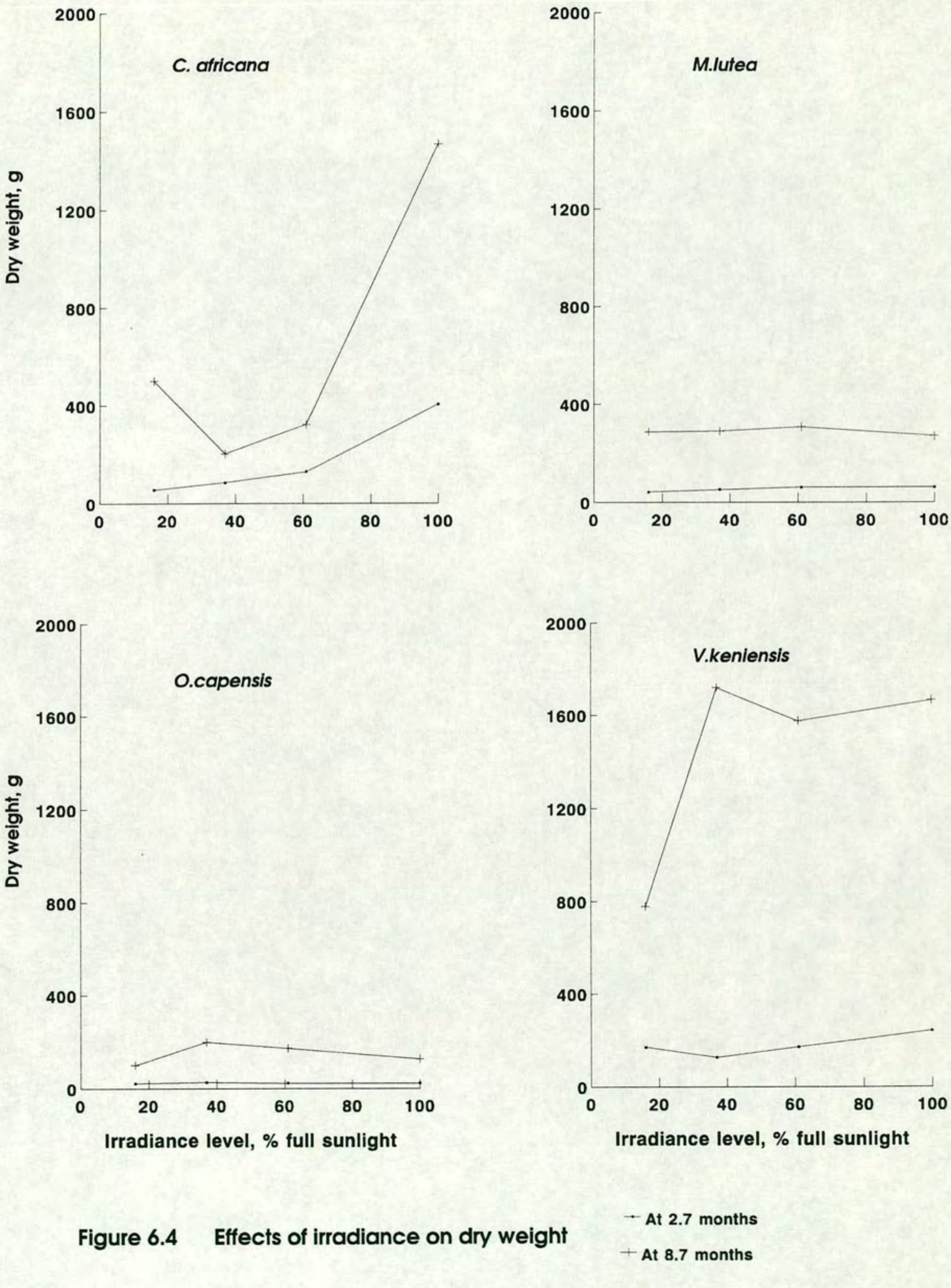

Figure 6.4 Effects of irradiance on dry weight

In the final harvest at 8.7 months, the dry weight of seedlings of *M. lutea* was also not affected by the irradiance treatments. In *O.capensis,* seedlings grown under moderate and light shade had significanly greater dry weight production than those grown under dense shade or full sunlight. In seedlings of *C. africana* the dry weight increased with increasing irradiance and was greatest under the full sunlight conditions. Although the seedlings of this species grown under the dense shade showed greater dry weight than those grown under moderate and light levels of shade, this was not significant. As shown in Table 6.3, there was a larger variation within the dry weight means of this species in seedlings grown under the dense shade. Variations within the means in the other treatments were also generally large in this species. During harvesting, large nodule-like swellings were observed in some seedlings of this species. Laboratory investigations showed that the swellings were a result of infection by root nematodes. This might have contributed to the greater variation in the growth *C.africana*. For *V. keniensis*, the dry weight was lowest under the dense shade. It increased rapidly under moderate shade and decreased slightly with further increase in irradiance (Figure 6.4). There were no significant differences in dry weight production between the seedlings grown under the moderate shade, light shade and full sunlight.

6.3.3 Leaf Number

In the final harvest, the leaf number was not significantly affected by the irradiance treatments but differences between the species were significant (Table 6.2). However, in all the species, the number of leaves increased with increasing irradiance up to the fifth month (Figure 6.5). Thereafter, the number decreased in all species except seedlings of *O. capensis* and *V. keniensis* grown under the dense shade. Seedlings of *O. capensis* had the greatest number of leaves in the final assessment while those of *C. africana* had the least. In the latter heavy leaf shedding occurred after the fifth month in seedlings grown under full sunlight. Some seedlings in this treatment started flowering during this period.

Table 6.3: Means and standard errors of some parameters in seedlings grown under different levels of irradiance in the clearing. Means were at 8.7 months for height, dry weight and number of leaves. Means for number of branches and crown width were at 5.1 months.

Light level	Species	Height, cm	Dry weight, g	Number of leaves	Number of branches	Crown width, cm
16 %	*C.africana*	87.4±36.3	500.2±425.2	37.5±36.4	2.7±1.3	119.5±49.9
	M.lutea	132.2±43.9	288.3±138.5	21.6±2.1	2.4±0.5	84.6±14.7
	O.capensis	89.2±10.8	100.0±20.6	82.9±10.4	6.3±0.5	52.4±4.2
	V.keniensis	203.4±3.1	778.6±389.6	66.6±26.6	3.8±1.2	139.2±16.6
37 %	*C.africana*	46..0±9.7	607.7±161.2	13.5±11.6	1.7±0.3	64.9±23.7
	M.lutea	98.8±19.8	291.1±62.3	25.5±1.1	3.2±0.5	68.2±6.0
	O.capensis	109.1±0.8	199.2±24.9	138.2±33.9	11.3±0.4	61.9±1.5
	V.keniensis	174.2±22.9	1719.2±369.2	46.6±19.4	7.0±3.3	131.8±19.0
61 %	*C.africana*	73.6±10.0	322.2±152.3	29.2±14.6	2.2±0.1	90.4±17.0
	M.lutea	82.9±22.6	308.3±106.1	32.3±8.9	2.9±0.5	64.9±10..6
	O.capensis	94.1±0.8	173.0±24.9	105.0±9.2	10.5±0.6	51.2±7.4
	V.keniensis	160.6±22.0	1575.0±423.5	51.7±11.0	8.8±3.2	123.7±16.3
100%	*C.africana*	107.1±13.7	1466.9±638.7	19.9±29.5	4.5±0.3	160.8±29.4
	M.lutea	62.6±26.5	271.1±209.8	30.9±7.2	4.1±1.5	52.2±9.3
	O.capensis	69.6±20.2	126.7±42.7	71.3±15.0	8.3±1.8	111.4±5.3
	V.keniensis	121.6±27.0	1664.4±647.3	43.9±29.4	12.6±3.9	118.4±15.4

6.3.4 Primary Branches

All species except *O. capensis*, showed the greatest number of primary branches under the full sunlight treatment (Figure 6.6). In the fifth month, the number of primary branches was significantly affected by the irradiance treatments and differences between the species were significant (Table 6.2.). Seedlings of *V. keniensis*, *M. lutea* and *O. capensis* had the lowest number of branches under the dense shade. Seedlings of *O. capensis* and *V. keniensis* both showed the greatest number of primary branches while those of *C. africana* showed the least. The number of primary branches in the latter was relatively high in seedlings grown under the full sunlight treatment compared to those grown under shade. Seedlings of *M. lutea* showed small differences in number of branches between seedlings grown

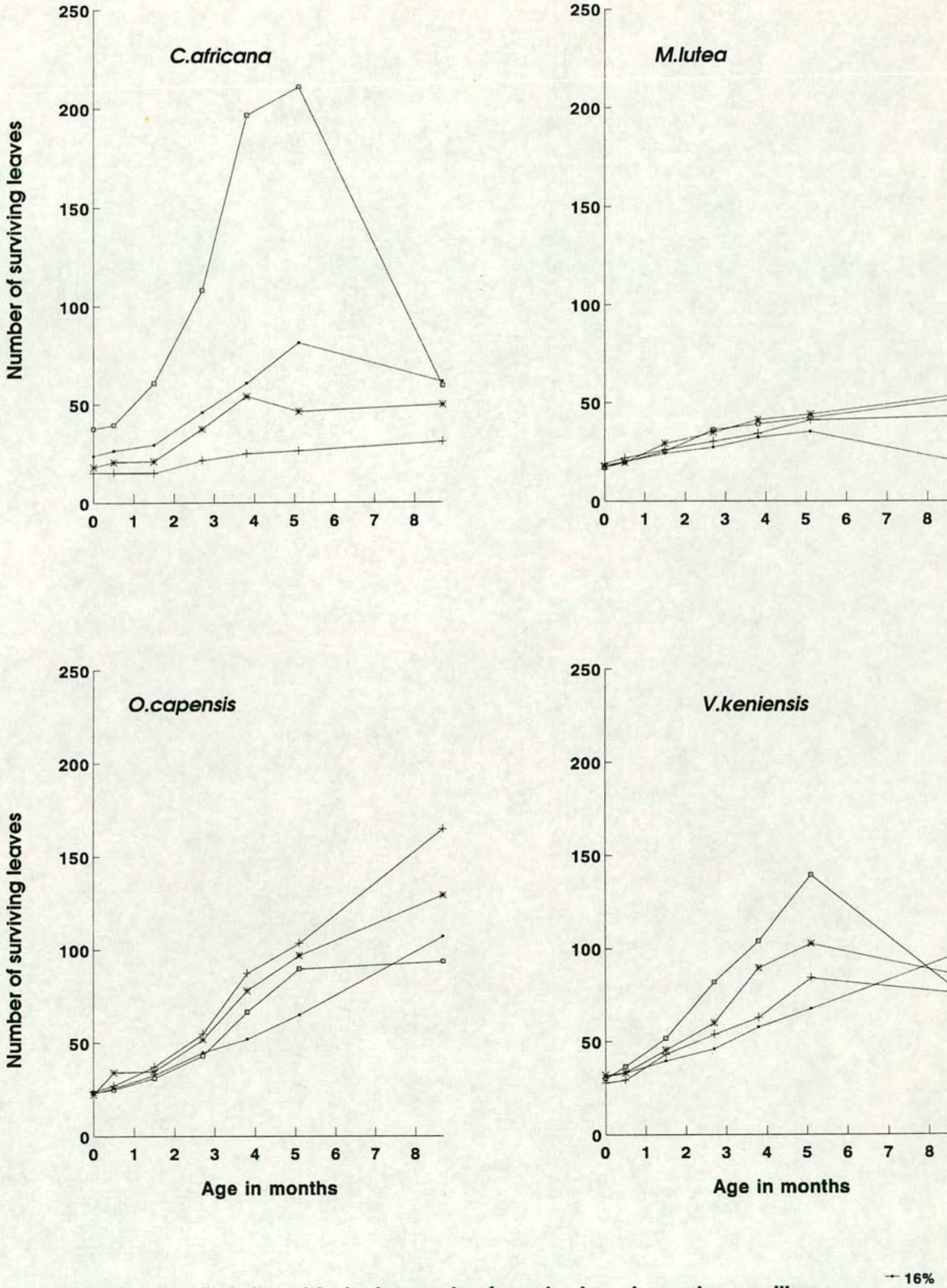

Figure 6.5. Relationship between leaf survival and age in seedlings grown under different irradiance levels.

under the four irradiance treatments. For *O. capensis*, seedlings grown under full sunlight had fewer primary branches than those grown under moderate shade levels.

6.3.5 Crown Diameter

After five months of growth, the crown diameter was not affected by the irradiance treatments but differences between species were significant (Table 6.2). Seedlings of *C. africana* and *V. keniensis* showed the largest crown diameters (Figure 6.7). In *C. africana* seedlings grown in the open displayed the largest crown diameter. In contrast, *V. keniensis* and *M. lutea* displayed the largest diameters in seedlings grown under the dense shade. Seedlings of *O. capensis* tended to display smaller crowns in seedlings grown in the open.

6.4 DISCUSSION

Before the experiment started, seedlings had grown for about three months under full sunlight. Construction of shade-houses in the shaded treatments was, therefore, similar to transferring seedlings from full sunlight to different levels of shade. Significant interactions in dry matter production after 2.7 months showed that the species differed in their initial responses to changes in the light availability. The significant interaction was due to the rapid increase in dry weight production in seedlings of *C.africana,* while those of *M.lutea* and *O.capensis* showed little growth. Seedlings of *M.lutea* grown under the full sunlight were initially browsed by grasshoppers and this probably affected its response. However, the slow initial growth response in *O.capensis* suggests that this species has low acclimation potential to changes in the light environment. The lower initial growth in dry matter production in seedlings of *C.africana* and *V. keniensis* confirms the observations in Chapter 4, which showed that these species acclimate slowly to a decrease in light availability.

Growth of seedlings of *C.africana* in the present study was relatively slow in comparison to the observations made under nursery conditions. Under nursery conditions, this species had greater growth (in RGR, biomass and height) than *V.keniensis*. In contrast, *V.keniensis* had greater growth than *C.africana* under all light levels in the clearing (Figures 6.3 and 6.4). The lower growth in *C.africana*

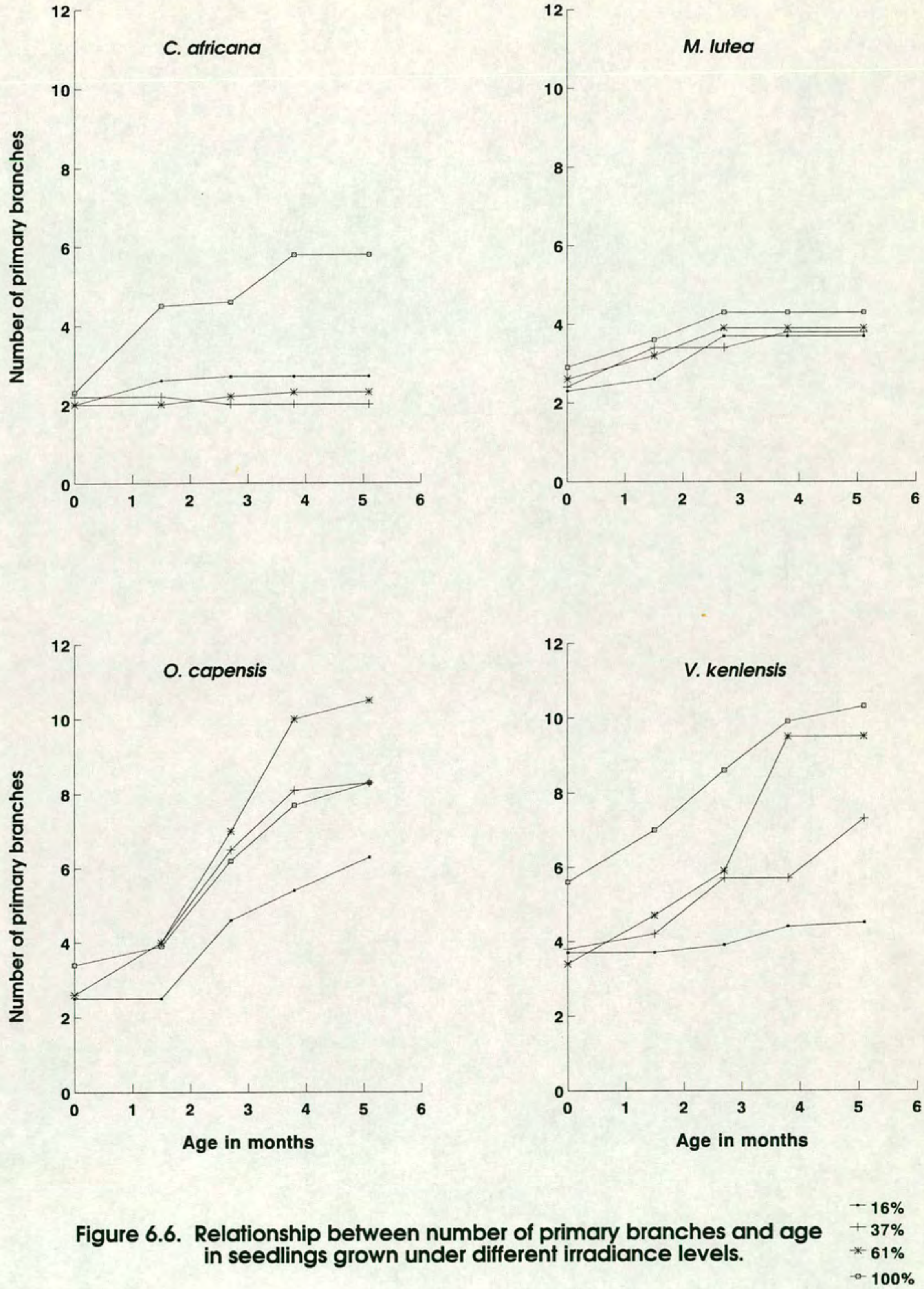

Figure 6.6. Relationship between number of primary branches and age in seedlings grown under different irradiance levels.

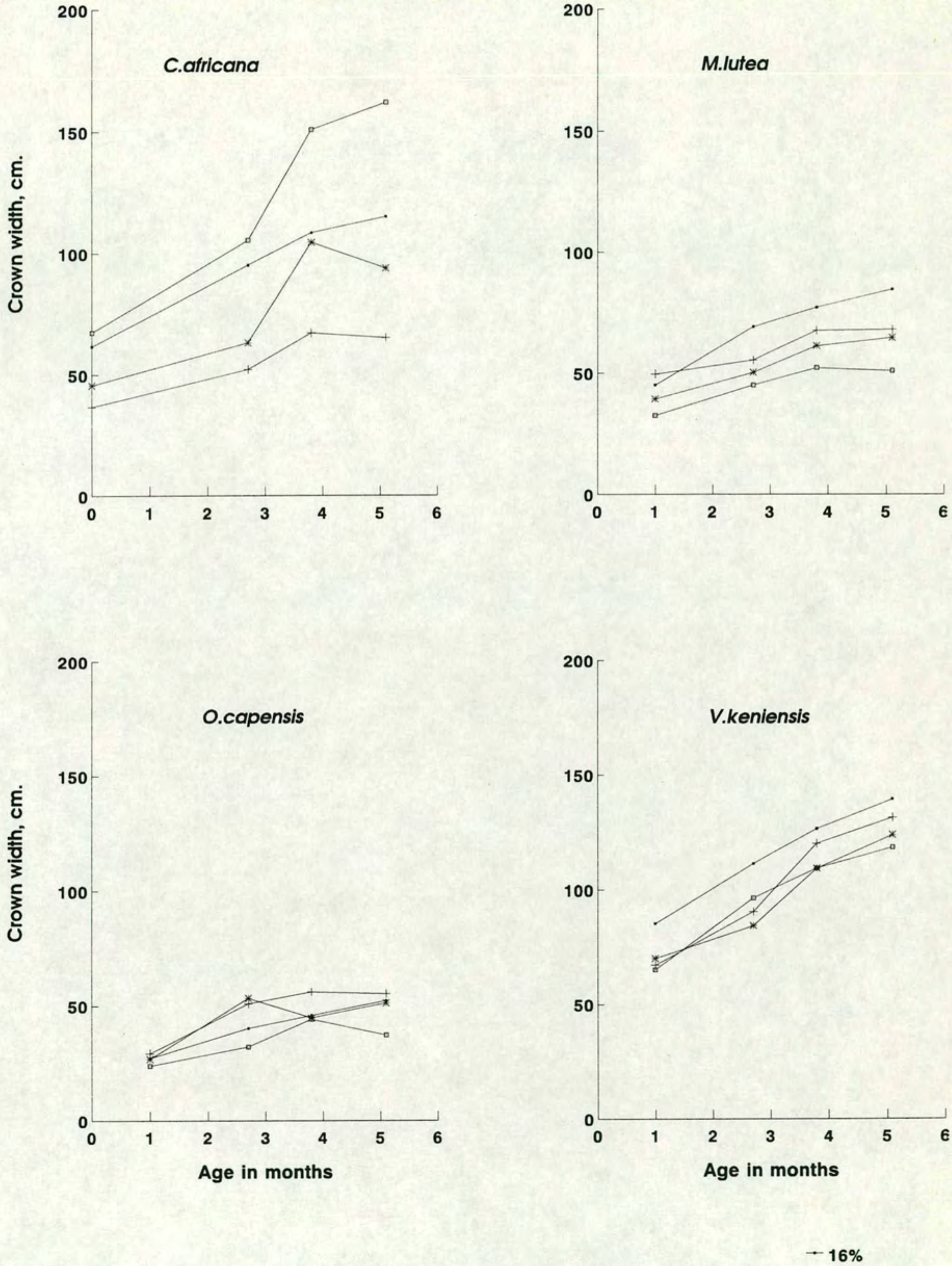

Figure 6.7. Relationship between crown width and age in seedlings grown different irradiance levels.

relative to that of *V.keniensis* was probably a result of several factors. First, as shown in Chapter 3, *C. africana* is more sensitive to moisture stress than *V. keniensis*. The four-month dry season, from June to September resulted in reduced height growth and heavy leaf shedding in *C. africana* (Figures 6.3 and 6.5). The dry season also affected the growth of *V. keniensis*, but this occurred much later and the effects were less. The presence of nematodes in the roots of *C. africana* might have affected the growth by interfering with water and nutrient uptake. This, however, did not affect all the seedlings and appeared to be random. In Chapter 3, it was shown that seedlings of this species grew slowly under low level of nutrients supply. The slow growth under shade might have been due to location of some of these treatments in soils which were low in nutrients.

The low soil fertility in the clearing and the long dry season resulted in reduced height growth of *C. africana* grown in all irradiance treatments. This seems to have occurred through shift in allocation of assimilates from the stem to the roots. The same observation was also made in Chapter 3. Under conditions of severe moisture stress survival probably became more critical than growth. Seedlings, therefore, had to invest in root development to exploit greater volume of soil for moisture and nutrients. It was possibly for this reason that no mortality occurred, although the dry period was long. However, reduced height growth in this species under conditions of moisture stress is likely to be disadvantageous if it is growing amongst other plants which are drought tolerant. By flowering early and showing high leaf turn-over, *C. africana* displayed characteristics common to pioneer species (Bazzaz, 1991 ; Whitmore, 1985 &1989). High leaf turn-over rates may facilitate rapid acclimation to new light environment by production of new leaves (Denslow, 1987) and may play an important role in nutrient cycling such as in agroforestry systems.

All the parameters measured were greatest under full sunlight in *C. africana.* This confirms the observations made in the nursery that the species is a strong light demander. However, its growth is likely to be limited by moisture and nutrient supply under field conditions. Growth responses of *C. africana* were, therefore, typical of pioneer species and were similar to those reported for *H. appendiculatus* (Fetcher *et al*, 1983), *Cecropia obtusifolia* (Popma and Bongers, 1988), *Acacia aulacocarpa* and *Toona australis* (Thompson *et al*, 1988) and *T. ivorensis* (Eamus *et al*, 1990). However, seedlings of *C. africana* did not show high mortality under the full sunlight treatment. This was in contrast to that reported for *H. appendiculatus* (Fetcher *et al*, 1983) and *T. ivorensis* (Eamus *et al*, 1990).

Biomass production increased rapidly in *V. keniensis* under field conditions in the clearing. This was not expected as this species had shown moderately slow growth under nursery conditions (Chapters 3 - 5). It seems that juvenile seedlings of this species show initial slow growth, but the growth rate increases once the seedlings are established in the field. Newly germinated seedlings of this species are therefore easily overtopped and shaded by faster growing colonisers. For this reason, *V. keniensis* is unlikely to be among the first species to occupy forest clearings, but should regenerate as a secondary species, once the faster growing colonisers start dying. Under shade, *V. keniensis* maintained rapid growth in height during the dry season. Observations during seedling excavation indicated that seedlings of this species had deeper vertically growing roots compared with seedlings of the other species. This rooting pattern enhances moisture absorption from the deeper layers of soil and this probably enabled the seedlings of *V. keniensis* extend their growth period. Seedlings of *V. keniensis* had greatest final dry matter production under moderate shade (37% of full sunlight). This level of irradiance simulates light conditions at the centre of a medium size or light canopy gap (Fetcher *et al*, 1983; Chazdon and Fetcher, 1984a & b). This suggests that *V. keniensis* might regenerate best in medium size forest gaps. It also seems to occur in large canopy gaps as indicated by the slight decline in growth under light shade and full sunlight treatments. This is in agreement with the observations made in the nursery (Chapter 3). In secondary succession, partial shade under dying colonising species is also likely to provide ideal conditions for the regeneration of *V. keniensis.*

The increase in height growth with decreasing irradiance (Figure 6.3) in *V. keniensis* was probably due to increased investment in stem growth, but at the expense of the development of branches, leaves (Figures 6.5 and 6.6) and possibly roots. The increased stem growth was probably as a result of the lower R:FR ratio (0.88) under the dense shade. This species had not, however, shown a marked stem elongation under a much lower R:FR (0.36-0.65) ratio in the nursery. A rapid stem growth in this species will enable its seedlings reach the upper strata of the canopy before the gap size is reduced by lateral growth of branches of the canopy trees. *V. keniensis* is, therefore, well adapted to medium size to large forest gaps.

The results of this study have shown that seedlings of *V. keniensis* require some moderate shading for optimum growth. This is in accordance with previous studies on growth of seedlings of some tropical trees Nicholson (1960), Fetcher *et al* (1983), Popma and Bongers (1988). In contrast to most of the previous field studies, seedlings of *V. keniensis* displayed a broader response to irradiance above 37% of full sunlight.

The dry matter production in seedlings of *M. lutea* was relatively low compared to those of *C. africana* and *V. keniensis* grown in all irradiance treatments. The dry matter production on *M. lutea* was unaffected by the light treatments. In seedlings grown under full sunlight, initial damage by the grasshoppers seem to have retarded the growth. In shade-grown seedlings, no clear explanation could be found for the lower growth. However, it is possible that some of the plots were located in poorer soils. Although the nutrient requirements of this species are not known, field planted seedlings of *M. lutea* sometimes show stunted growth and this could be related to low soil fertility or high irradiance.

Height growth and biomass allocation patterns in *M. lutea* were similar to those of *V. keniensis*. In *M. lutea*, however, increased stem growth resulted in fewer number of branches and leaves, indicating that this species also showed some response to the slightly lower R:FR ratio under the dense shade. These results suggest that *M. lutea* is likely to grow under similar light environment as *V. keniensis,* in medium size and large canopy gaps. Although *M. lutea* is usually grown in the open, under high irradiance, it does not seem to be a strong light demander.

The patterns of height growth and dry weight production in *O. capensis* were similar to those of *V. keniensis.* However, growth in *O. capensis* was considerably lower compared to that of *V. keniensis* (under all irradiance treatments) and that of *C. africana* (under full sunlight). This indicates that *O. capensis* is a slow growing species, which seems to regenerate in medium size forest gaps, receiving irradiance level of about 37% of full sunlight. Because its growth in dry weight and height declined at light levels above and below 37% of full sunlight, *O. capensis* is likely to be confined to medium size canopy gaps. These results are in contrast to the observations made by Eggeling (1947) who reported this species as among those found in colonising forests in Budongo, Uganda. Parry (1957) reported that *O. capensis* is liable to sunscorch although it is capable of growing under full sunlight. This observation seems to confirm the findings in this study, that this species is not a pioneer. Although seedlings of *O. capensis* persist under closed natural forests in Kenya, saplings of this species are rare. Mature trees of *O. capensis* are, however, among the emergents in natural forest. The growth response of *O. capensis* is comparable to that reported for a shade-tolerant *Pentaclethra macroloba* (Oberbauer and Strain, 1985). Similar responses have also been reported in nursery-grown seedlings of *Afrormosia elata* (Ampofo and Lawson, 1972), *Shorea assamica, Hopea helferi* and *Vatica odorata* (Sasaki and Mori, 1981) and *Brachylaena huillensis* (Kigomo, 1990).

The crown width was unaffected by the light treatments, but in all species, it increased with increasing height of the seedlings. Since *C. africana* had greatest height growth under full sunlight and the other species under shade, this contributed to the significant interaction between the light and species treatments in crown diameter. In early stages of forest succession, larger crown width enables a seedling to pre-empt the site, and thus increases its competitive ability against fast growing colonisers.

In general, branching in the four species increased with increasing irradiance and seems to be negatively correlated with height growth. Increased branching is usually caused by reduced apical dominance (Meyer and Anderson, 1952; Kramer and Kozlowski, 1960; Street and Öpik,1984; Salisbury and Ross, 1978). It seems that in seedlings grown under full sunlight, high irradiance and/or moisture stress weakened or damaged the apical buds. This stimulated the development of lateral buds and increased the branching. However, in *M. lutea* branching was light. This species has the characteristics of developing few branches even in trees exposed to full sunlight. Increased branching has survival value, for it allows one of the side branches to grow as the main leader when apical shoot is damaged (Salisbury and Ross, 1978).

6.5 CONCLUSIONS

The four species generally showed differences in their light requirements. In *C. africana,* growth in height was faster under full sunlight than under shade. This species also flowered early, in less than a year after planting. According to Whitmore (1985 & 1989) some of the characteristics of the light demanding or pioneer species include fast height growth in the open areas and early flowering. *C. africana,* therefore, seems to fit well into the ecological group of the light demanding species. Growth in height in the other three species (*M. lutea, O. capensis* and *V. keniensis*) was generally highest under moderate shade, suggesting that they are neither light demanders nor shade tolerant.

Since *C. africana* displayed the greatest growth under full sunlight, it seems suitable for planting in clearings or in open areas. However, growth will be reduced under conditions of moisture stress. It is not suitable for planting into small or medium size canopy gaps. *V. keniensis* grows faster under moderately shaded conditions. Under full sunlight, height growth will be severely reduced because of increased allocation of assimilates to branches and roots. It is suitable for planting into large canopy gaps such as those caused through selection felling. *M. lutea* was not affected by the light treatments and appears suitable for planting under a wide range of light environments. However, further investigations are required to confirm the light requirements of this species. For increased stem growth, it should be planted under shaded conditions. *O. capensis* was the most shade-tolerant among the four species. However, it is not entirely shade-tolerant and appears only suitable for planting into light or medium size canopy gaps. It is neither suitable for planting in small gaps nor in clearing and open areas.

CHAPTER 7

SURVIVAL AND GROWTH OF PLANTED TREE SEEDLINGS UNDER A FOREST CANOPY

7.1 INTRODUCTION

The irradiance levels beneath primary moist tropical forests usually varies from less than 1% to about 4% (Richards, 1952; Stoutjesdijk, 1972; Longman and Jeník, 1984; Chazdon and Fetcher, 1984). Seedlings of tree species respond differently to this low irradiance. Those of shade tolerant species are able to survive or persist and grow under this level of light while those of the pioneer species cannot (Fetcher *et al.* 1984; Augspurger, 1984; Whitmore, 1984 and 1989; Popma and Bongers, 1988). However, tree species basically fall along a continuum in their light requirements (Augspurger, 1984).

In some tropical countries, attempts have been made to improve the stocking of depleted valuable species by enrichment planting. This involves the planting of seedlings in lines or gaps cut in a forest canopy. Such gaps need to be repeatedly kept open to allow the seedlings to get enough light and this is expensive (Whitmore and Bowen, 1983). This method has met with little success mainly because of inadequate understanding of the light requirements of individual species. Without this information, it is not possible to identify the most appropriate species and the size of the gap that needs to be kept open.

In Kenya, studies on the responses of tree seedlings to shade beneath forest canopies are scanty. In an enrichment trial planting, Kigomo (1987) observed that most species showed moderate growth, but low survival. In his study on the influence of shade on growth of seedlings of *Brachylaena huillensis*, Kigomo (1990) found more seedlings in small gaps receiving light levels of 2 to 14% of full sunlight, less in large gaps and hardly any in completely open sites. In contrast, Augspurger (1984) reported that seedlings of 18 Panamian species survived better in the sun than in the shade. In the shade, the more shade-tolerant species had a lower proportion of seedlings dying from diseases. All species grew better in the sun.

Sasaki and Mori (1981) grew potted seedlings of various species on the forest floor under different light levels ranging from 2 to 15% of full sunlight. They found that the growth of seedlings increased with increasing irradiance. However, they did not report on the effects of shade on survival. Fetcher *et al* (1983) found that in shaded conditions with irradiance level of 1.4% of full sunlight, seedlings of a pioneer species *H. appendiculatus* had survival rate of 49% while those of a shade-tolerant *D. panamensis* had 100% survival. Biomass of both species was lower under shaded conditions than in the sun. In their study on the effects of the canopy gaps on growth and morphology of ten seedlings of tropical trees, Popma and Bongers (1988) observed that growth of all species was enhanced in gaps but some species displayed relatively high growth rates in both shade receiving 0.9 to 2.3% of full sunlight and under full sunlight conditions.

The present study was carried out to determine whether seedlings of some valuable species in Kenya can survive and grow under heavy shade beneath a forest canopy. The species tried were *C. africana*, *V. keniensis, M. lutea* and *O. capensis*. These species have been over-exploited in most forest areas where they occur and their regeneration is poor. However, seedlings of *O. capensis, Prunus africana* and *Fagara macrophylla* seem to regenerate well beneath plantations of *V. keniensis* in Chuka Forest Reserve. The hypothesis was that plantations of *V. keniensis* provide environmental conditions suitable for regeneration of shade tolerant species.

7.2 MATERIALS AND METHODS

7.2.1 Location and site characteristics

This study was carried out in a plantation of *V. keniensis* located in Compartment 1 (L) in Kiamuriuki Forest Block of Chuka Forest Reserve. The plantation is 0.5 km from the natural forest and is situated 5 km west of Chuka Forest Station. It stands at an elevation of 1780 a.s.l and the site climate is similar to that described for Chuka forest in Chapter 2. The experiment was laid out on a gentle slope facing south.

When the experiment was set up, the plantation was 14 years old. It was initially planted at a spacing of 2.0 by 2.0 m or 2 500 stems per hectare (s.p.h.). and had been pruned to a height of 2 m at 6 years. Although it had not been thinned, tree losses as a result of severe competition and probably poor or moderate establishment in the early years, had reduced the stocking to between 1100 and 2000 s.p.h. The average height and diameter at breast height (d.b.h.) of the trees were 13.6 m and 13.2 cm respectively. The ground lacked the herbaceous layer except in areas with moderate stocking or near firebreaks. Saplings of *Xymalos monospora,* a seemingly shade-tolerant species, also occurred as undergrowth in scattered patches. Because *V. keniensis* is a deciduous tree (Section 2.2.2) which also displays self-pruning, the forest floor was mostly covered with its leaf litter and dead fallen branches. Plantations of this species shed the leaves continuously but the peak period is towards the end of the dry season in September/October. The trees are usually in full leaf in January to March.

7.2.2 Treatments and Experimental Design

The treatments were four species: C. africana, V. keniensis, M. lutea and *O. capensis.* The design was a complete randomised-block with five replicates. The blocks were laid along the slope but scattered within the plantation. Two of the replicates (Blocks I and II) were however only 10 m apart. The rest were 50 to 70 m apart and away from the two adjacent blocks. Each plot within the block had 25 seedlings of each species planted at spacing of 2.0 by 1.0 m and in a 5 x 5 arrangement.

Seedlings of each of the above species were from the same lot as those used in the previous experiment. Seedlings were raised using the methods described in Section 6.2.3.

7.2.3 Site Preparation and Planting

One replicate of this experiment (Block IV) was located in a site with a light undergrowth of herbs and saplings of *X. monospora*. There was no undergrowth in the other replicates. Site preparation was carried out during the dry season in September 1992. The light undergrowth in Block IV was cleared and pitting was done in all the blocks. Large pits (30 cm in depth and 30 cm in width) were dug and the roots of the mature trees severed to reduce root competition. The pits were refilled after one month. This allowed the tips of the severed roots to dry up and reduce their rates of recovery.

other hand, those of *C. africana* were yellowish and had lost about a third of their leaves. No weeding was carried out as the plots remained free of undergrowth. Falling leaves provided good mulch for the seedlings and the soil at the forest floor was moist up to the end of the experiment, except towards the end of the dry season in October 1993. A guard protected the plots from cattle which occasionally grazed along the firebreaks and on poorly stocked areas of the forest.

7.2.4 Measurements of Microclimate

To characterise the microclimate in the plantation, data on PPFD, temperature and VPD were collected twice for 6 days in February and 9 days in May/June, 1993. On both occasions, measurements were taken in two adjacent Blocks I and II. The instruments and methods used were similar to those described in Chapter 2. However, three quantum sensors were used: one at the centre of Blocks I and II and the third one was placed above the canopy. The sensors beneath the canopy were placed at the height of 20 cm above the ground. The temperature and the VPD were only measured beneath the canopy at the centre of the two blocks. The psychrometric units were also placed at the same level as the quantum sensors. In October 1993, instantaneous PPFD was measured for one day using two hand-held quantum sensors (Skye Instruments, Ltd. Powys, U.K.). Simultaneous measurements (inside and outside the forests) at about noon, but on a partly cloudy day. Light quality was measured using the same instruments as described in Section 4.2.3. Measurements were made for one day in January, February, July and August, 1993. This was done at about noon, local time. Twenty simultaneous readings were taken in each block. The sensors were interchanged half-way in between the readings. Rainfall was recorded at the station from January to December 1993.

Table 7.1 and Figure 7.1 show the mean values and daily variation in PPFD beneath and above the canopy.

Table 7.1 Mean daily PPFD ($\mu mol\ m^{-2}\ s^{-1}$) below and above the canopy in 6 days of February and 9 days of May/June 1993

Month/Average	Beneath canopy	Above canopy	Beneath canopy % full sun
February	20.8	928.2	2.24
May/June	4.7	758.3	0.62
Mean	12.8	843.2	1.47

The seedlings received low irradiance levels which were comparable to those found in understorey habitats of tropical forests (Richards, 1952; Stoutjesdijk, 1972; Longman and Jeník, 1987; Sasaki and Mori, 1981; Chazdon and Fetcher, 1984). The irradiance levels received below and above the canopy in May/June were lower than those recorded in February. This was a result of the usually lower solar radiation in this area in May to August (Figure 2.1). During the one day measurements in October 1993, PPFD recorded were 214.8 and 809.5 μ mol m^{-2} s^{-1} inside and outside the forest respectively. The PPFD level inside the forest was 25% of that in the full sun. The increase in irradiance was due to increased leaf shedding. The forest canopy affected the light quality. In the open, the R:FR ratio was almost constant at a value of 1.04. However, below the canopy the values were moderately low. In January and February the R:FR ratios below the canopy were 0.44 and 0.41 respectively. In July, the value was the same as that recorded in January, but increased to 0.67 in August. This increase was as a result of increased leaf shedding. Lee (1989) reported lower values of 0.22 to 0.33 in a semi-deciduous tropical forest when the trees were in full leaf and a value of 1.10 when most of the trees had shed their leaves. Chazdon and Fetcher (1984) recorded R:FR ratios of between 0.17 and 0.69 under deep shade in tropical rain forests. Since the irradiance level below the canopy of the *V. keniensis* plantation was comparable to those reported beneath the canopy of tropical forests, the R:FR ratio was relatively high even when the trees were in full leaf. This seems to suggest that the single forest canopy of the plantation showed less filtering effects on the red light compared to multistorey canopies of natural forests.

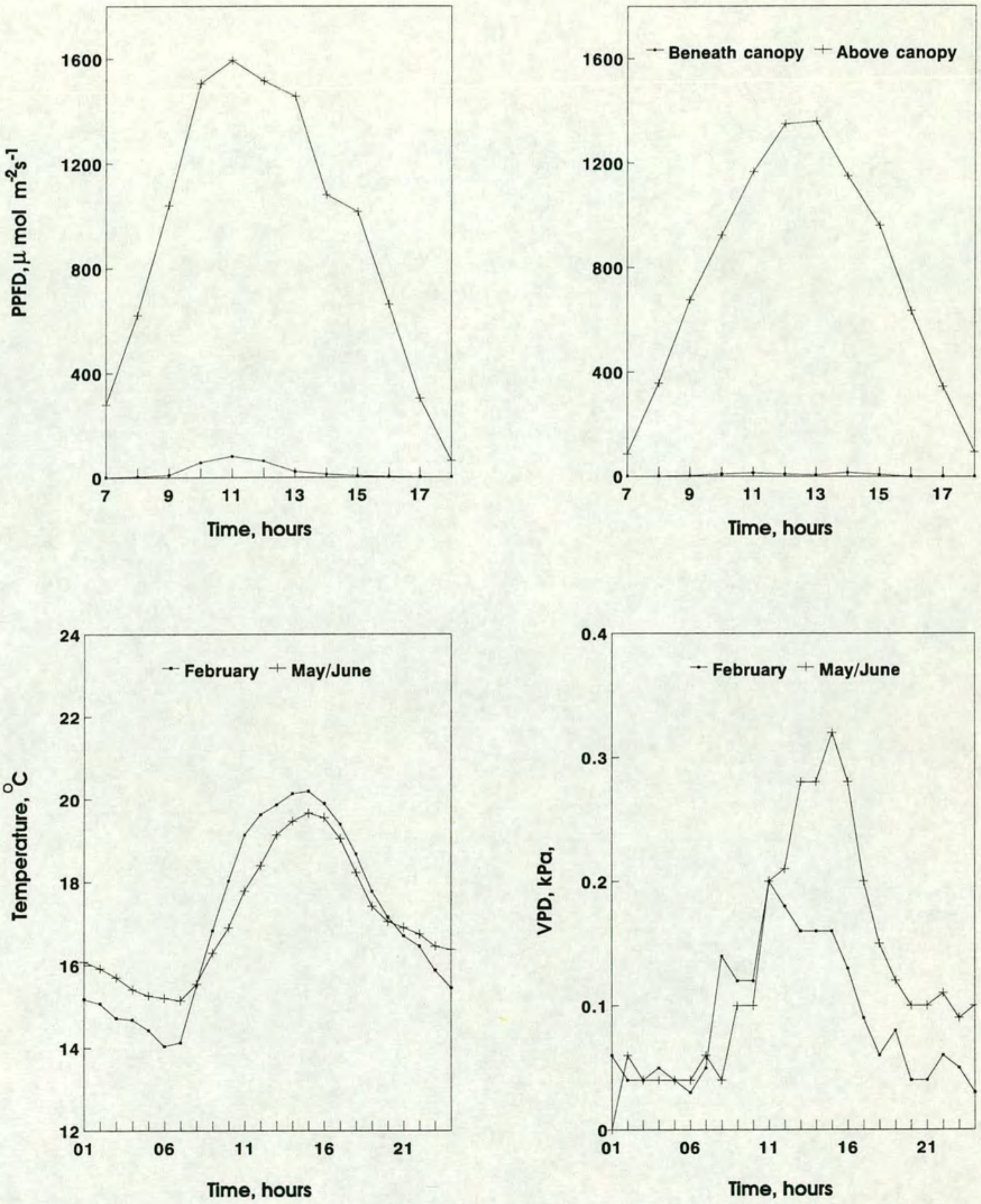

Figure 7.1. Variation in mean daily PPFD, temperature and VPD in 6 days of February and 9 days of May/June 1993. Top: PPFD below and above the canopy in February (left) and May/June (right). Bottom: temperature (left) and VPD (right).

As shown in Figure 7.1, there were small differences in diurnal temperature variation below the canopy in the months of February and May/June. The mean value was 17.1 °C in February and 17.1 °C during May/June. This suggests that the temperatures beneath the canopy showed little variation for most of the year. Although it was not measured, the mean daily temperature above the canopy was probably 4 to 5 °C higher than that below the canopy. Figure 7.1 shows the daily variation in vapour pressure deficits in February and May/June. In February, the mean value was 0.09 kPa while in May/June, it was 0.13 kPa. The small differences in vapour pressure deficits occurred mostly in the afternoons. These differences seemed to be related to the differences in rainfall received in the months of January/February and May/June. Rainfall variation for 1993 is shown in Figure 7.2.

7.2.5 Data Collection and Analysis

Seedling survival and number of leaves were assessed almost monthly for 15 months. In each assessment, visual observations on the conditions of the seedlings were also made. All surviving seedlings were assessed in each plot. At the end of the experiment, after 15.3 months, all seedlings were excavated for dry weight determination. All the plant parts of seedlings from each plot were kept together and samples were oven-dried to constant weight. Height increments and leaf gains or losses between the initial and final assessments were computed. ANOVA was carried out on percentage survival (after arcsin transformation), height increments, leaf number and dry weight values.

7.3 RESULTS

7.3.1 Survival

There were significant differences in seedling survival among the species (Table 7.2). *O. capensis* showed 100% survival and only one seedling died in *M. lutea*. *C. africana* showed the lowest survival of 30.4%. The survival of *V. keniensis* was moderate but significantly better than that of *C. africana*. In *C. africana* and *V. keniensis*, the mortality was continuous (Figure 7.3). One month after the start of the experiment, some seedlings of *C. africana* had been attacked by termites in one plot, while in another plot, leaves had been cut off by an unknown animal. The

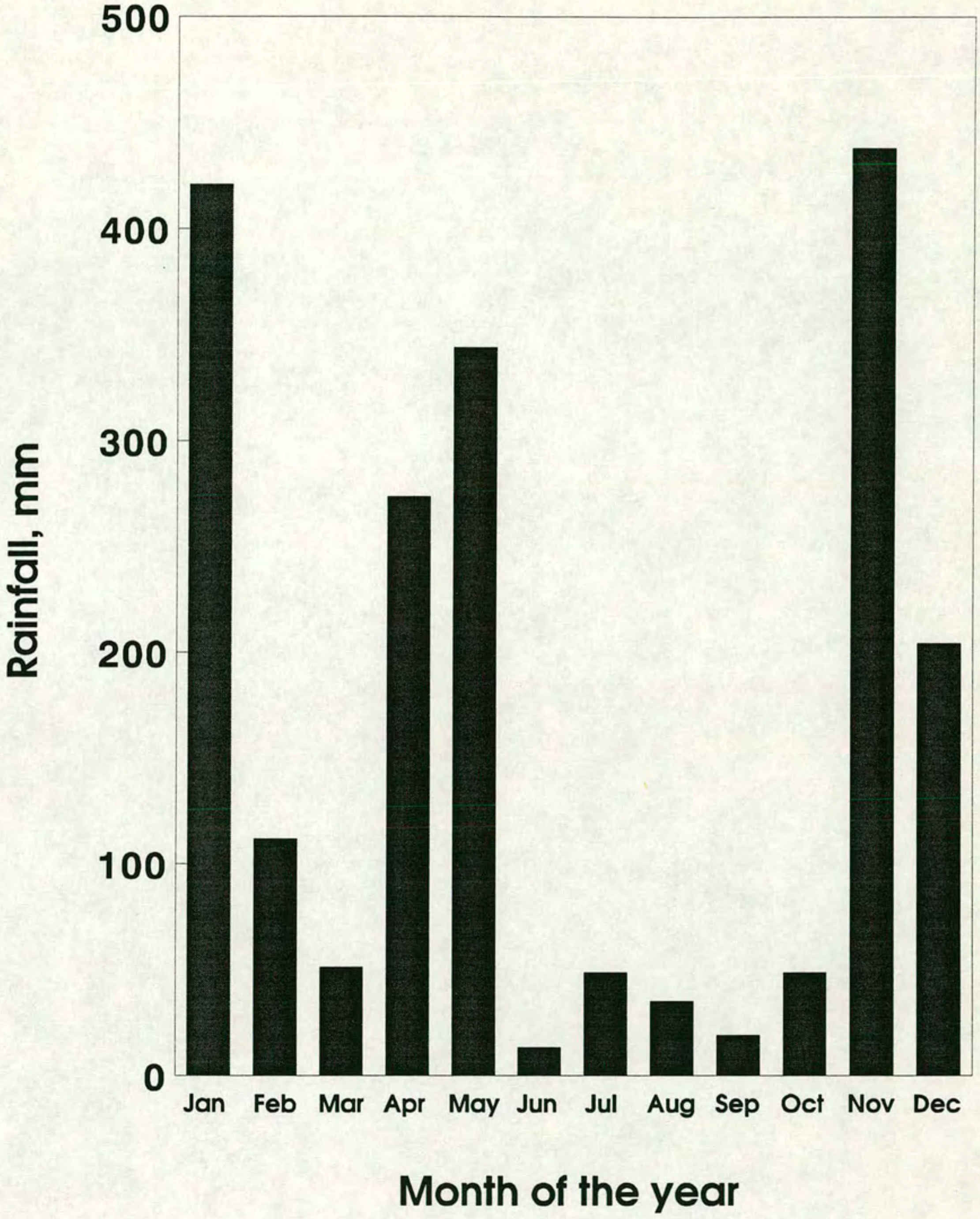

Figure 7.2. Rainfall distribution at Chuka Forest Station from January to December 1993.

Table 7.2: Mean Survival, height increment, dry weight and leaf gain or loss in seedlings of the four species grown beneath a forest canopy. The means were at the end of the experiment at 15.3 months.

Species	Survival %	Height increments (cm)	Dry weight, g	Leaf gain/loss number
C. africana	30.4	41.3	16.3	2.1
M. lutea	99.2	36.8	33.5	9.5
O. capensis	100.0	32.9	20.0	18.6
V. keniensis	68.0	10.7	6.4	-3.7
Level of Significance	****	***	***	****
L.S.D. at P < 0.05	7.2	12.0	9.6	4.3

For details see Appendix VI

*** = Significant at P<0.001

**** = Significant at P<0.0001

affected seedlings died later. The mortality of seedlings in *C. africana* and *V. keniensis* occurred in the first and about five months after planting respectively. In both species the mortality increased steadily up to the end of the experiment. In these species, mortality generally occurred after the seedlings had lost all their leaves. Some seedlings also died following terminal or/and stem rot possibly caused by fungal infection. In other cases, falling dead branches from the upper canopy trees also damaged the seedlings, but this affected all species. Towards the end of the dry season, some seedlings of *O. capensis* showed signs of wilting but none of them died.

7.3.2 Height Growth

As shown in Table 7.2, there were significant differences in height increment between the species. Seedlings of *C. africana* and *V. keniensis* showed the largest and the lowest increments respectively. Height growth generally increased with time (Figure 7.4). Soon after planting, seedlings of *M. lutea* produced dormant buds resulting in low increment. In seedlings of *V. keniensis*, height increment was minimal during the duration of the experiment. In the other species the increments were moderate during the first 12 months, but increased more rapidly thereafter especially in seedlings of *C. africana*.

7.3.3 Dry Weight

The differences between the species in dry weight production were significant (Table 7.2). Seedlings of *M. lutea* had the highest dry weight and those of *V. keniensis* had the lowest (Figure 7.5). There were no significant differences in dry weight between the seedlings of *C. africana* and *O. capensis*. Seedlings of *M. lutea* had about 1.7, 2 and 5 times greater dry weight than those of *O. capensis, C. africana* and *V. keniensis* respectively.

7.3.4 Leaf Number

Leaf number was not the cumulative number of leaves produced during the duration of the experiment. It was the difference between the number of leaves at the start and the end of the experiment. This leaf gain or loss differed significantly between the species (Table 7.2). Seedlings of *O. capensis* had the highest leaf gain while those of *V. keniensis* displayed net leaf loss. Leaf gain generally increased with time in seedlings of *O. capensis* and *M. lutea* (Figure 7.6). It was rapid towards the end of the experiment in seedlings of *O. capensis*. Leaf gain in seedlings of *C. africana* occurred in two peaks which generally coincided with the rainy seasons and the time when upper canopy trees had lost most of the leaves. Leaf loss in seedlings of *V. keniensis* almost followed the same pattern as that of seedlings of *C. africana*. In both species, seedlings had the lowest number of leaves in September/October 1993 which was the peak of the dry season.

Insect herbivory was observed in seedlings of *C. africana* and *V. keniensis* in the first month after planting. Leaves of most seedlings, especially in those of *V. keniensis* had many holes or perforations caused by leaf skeletonisers and leaf miners. Insect defoliation tended to increase when illumination was higher on the forest floor. Herbivory was moderate to severe in seedlings of *V. keniensis* as the same insects also usually feed on the leaves of mature trees, just before leaf shedding. The damage in seedlings of *C. africana* and *M. lutea* was light. Seedlings of *O. capensis* were neither affected by insect herbivory nor fungal infection.

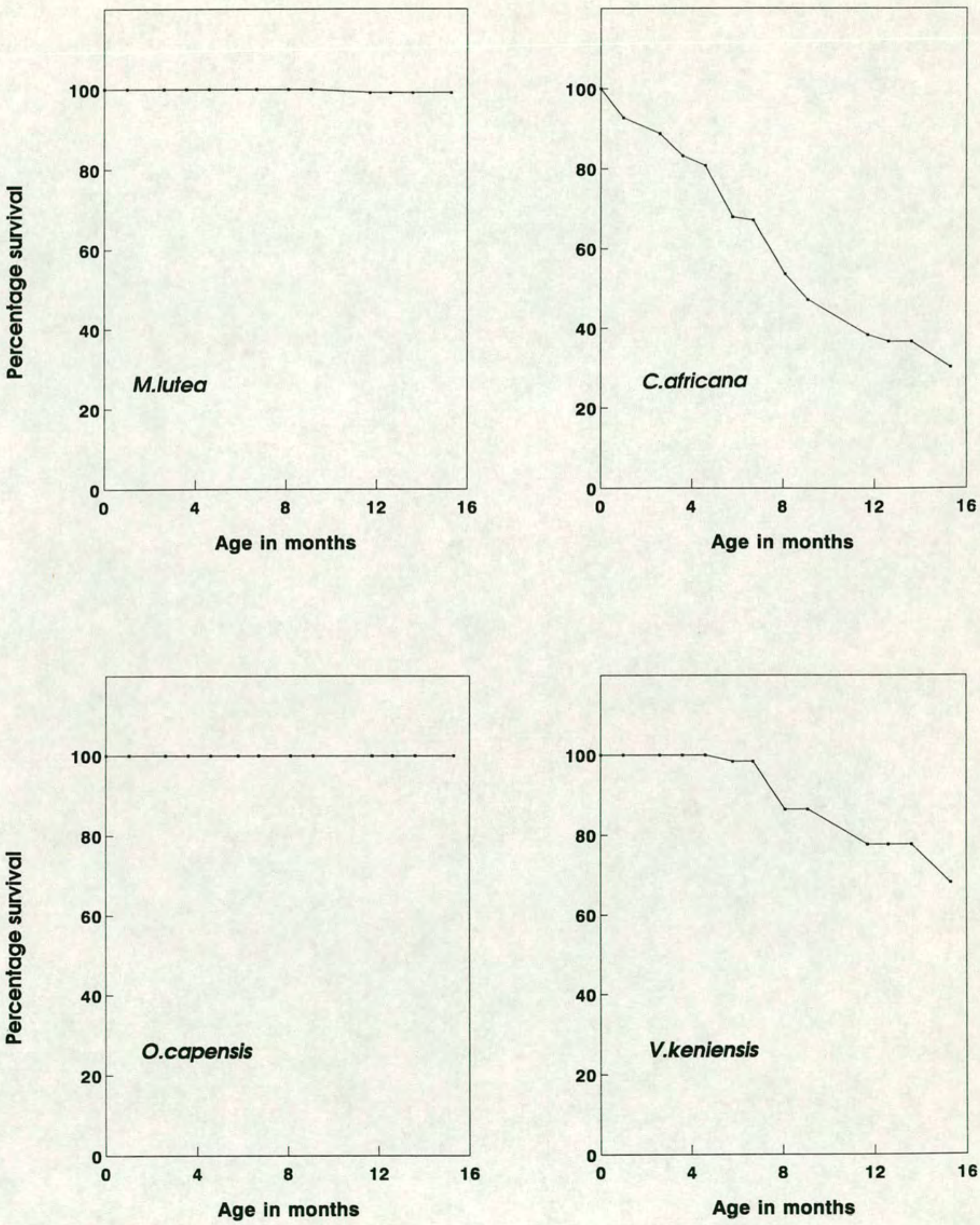

Figure 7.3. Relationship between survival and age of seedlings grown under a plantation of *V.keniensis* for 15.3 months.

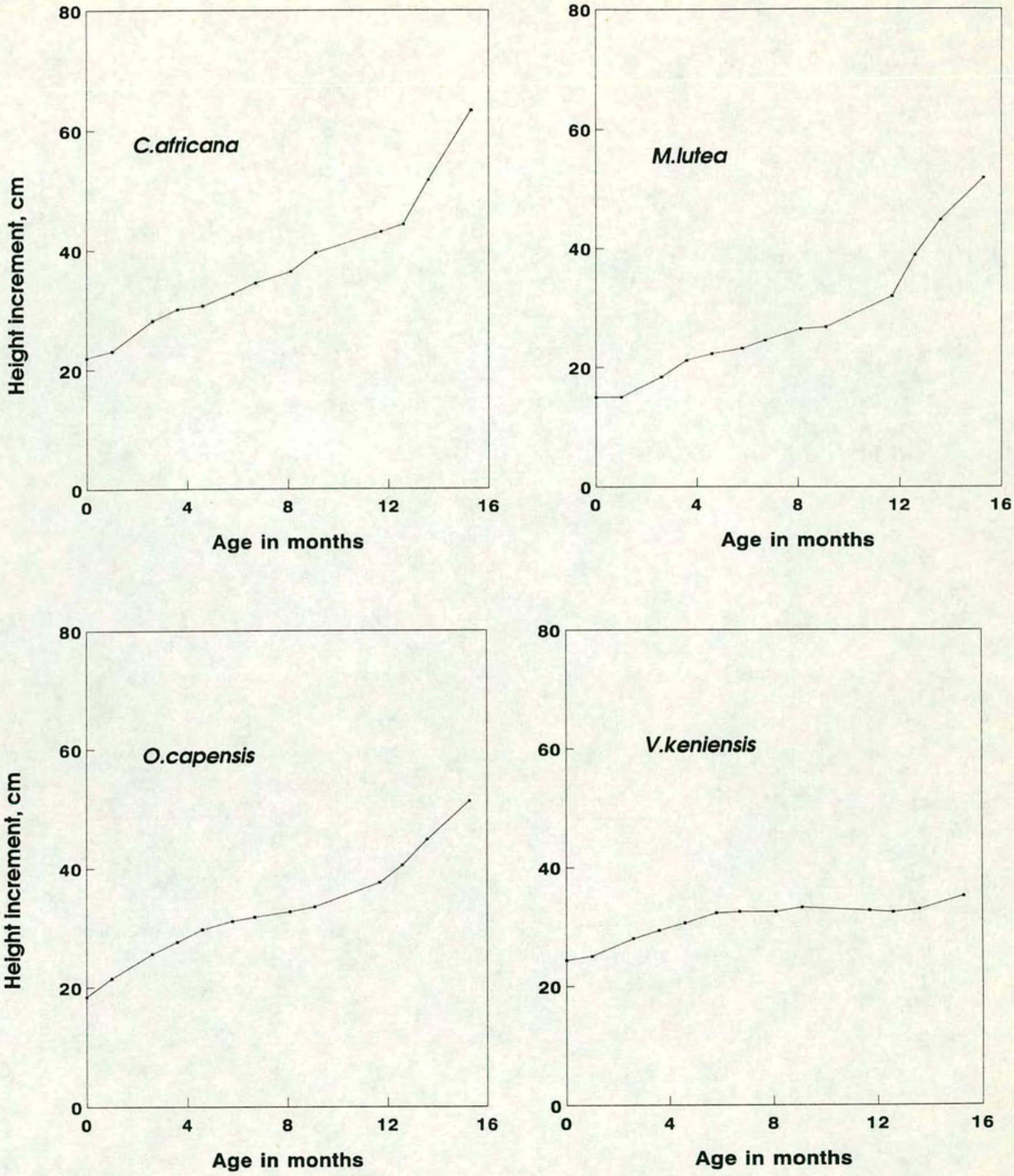

Figure 7.4. Relationship between height growth and age of seedligs grown for 15.3 months in a plantation of *V.keniensis*.

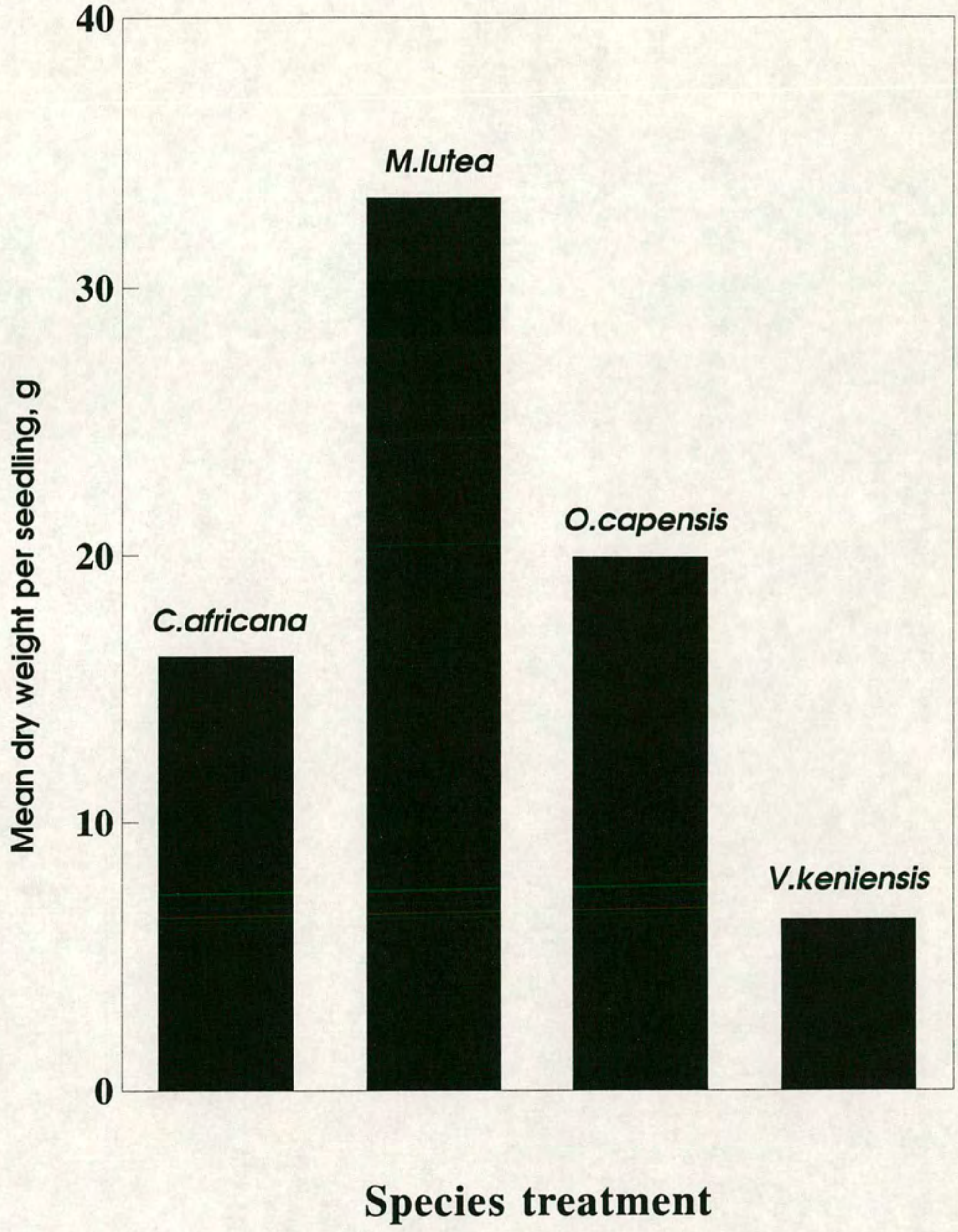

Figure 7.5. Dry weight of seedlings of the four species harvested after growing for 15.3 in a plantation of *V.keniensis*.

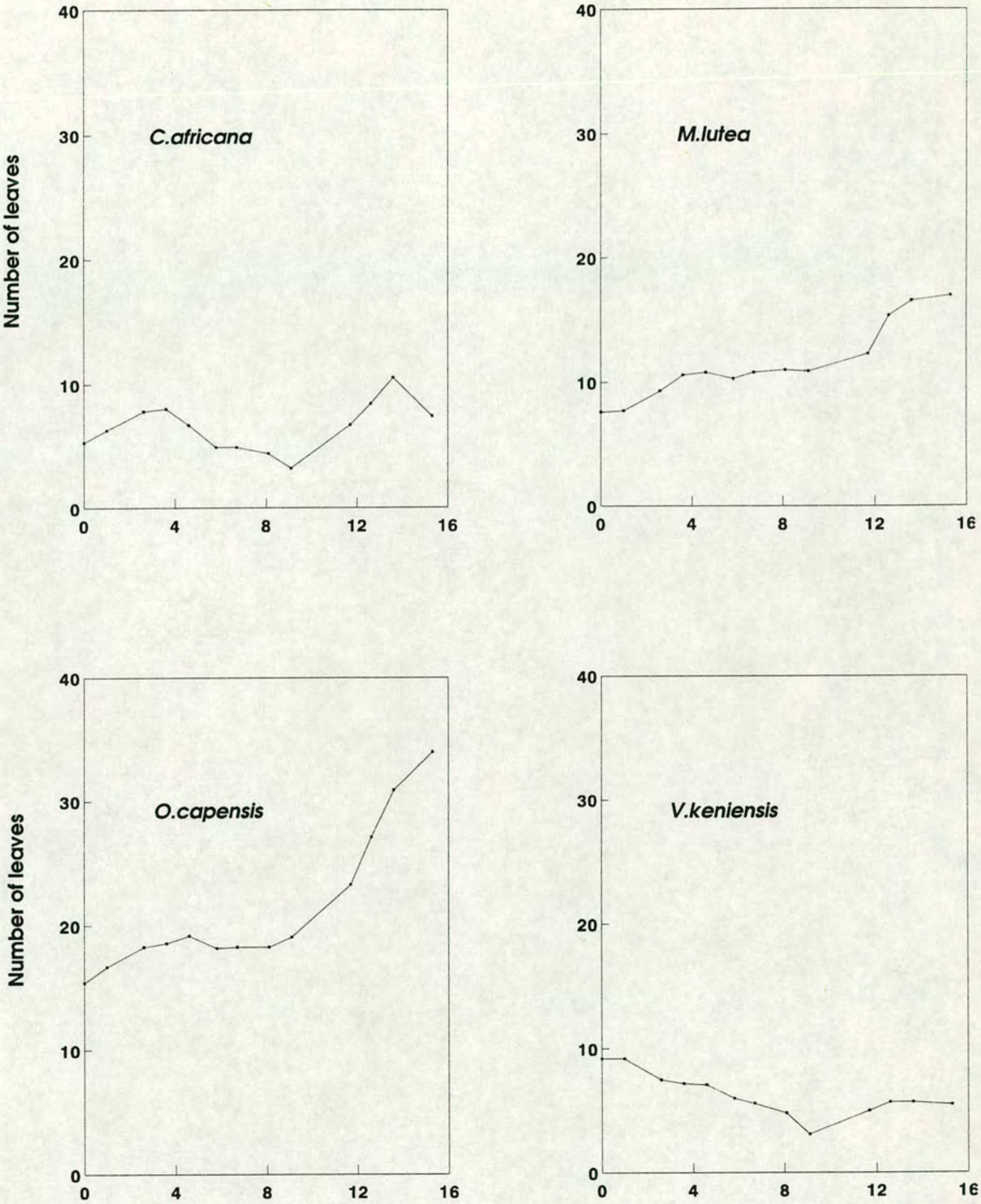

Figure 7.6. Number of leaves gained or lost per seedling in plants grown for 15.3 months under a plantation of *V.keniensis*.

7.4 DISCUSSION

Seedlings in this study had been grown under full sunlight in the nursery before planting under the canopy. The irradiance level below this canopy was generally comparable to that on the forest floor of tropical forests. The results have shown that the four species grew slowly under the heavy shade, but there were marked differences among them in survival. While *M. lutea* and *O. capensis* persisted, high mortality was observed in the other two species, especially in *C. africana.* Growth was also particularly poor in *V. keniensis.*

High mortality in seedlings of *C. africana* and *V. keniensis* seems to be the result of several factors, which include: low irradiance, poor conditions of the seedlings at planting, drought or competition from roots of the canopy trees, herbivory and attack by fungal pathogens. It was shown earlier in Chapter 4 that seedlings of *C. africana* and *V. keniensis* lost their leaves when transferred from the full sunlight to dense shade (13% of full sunlight). Since open-grown nursery seedlings were transferred to deep shade (1.5% of full sunlight) in the present study, these pioneer or gap species were probably unable to maintain positive carbon balance, resulting in poor growth, leaf losses and seedling mortality. Because seedlings of *C. africana* were rather unhealthy at planting, this also limited their ability to acclimate to the large decrease in irradiance and this might have been the cause of earlier deaths. On the other hand, it seems that seedlings of *M. lutea* and *O. capensis* maintained positive carbon balance under the deep shade and this probably contributed to their high survival. This seems to confirm the observation in Chapter 6, which showed that *M. lutea* and *O. capensis* are relatively more shade tolerant than either *C. africana* or *V. keniensis*.

Leaf defoliation by herbivorous insects was probably the most important cause of seedling mortality in *C. africana* and *V. keniensis.* By mining or perforating the leaf lamina, the insects reduced the leaf areas. Many holes in the leaves also probably interfered with the transport of water, nutrients and assimilates in the plants. Reduced leaf area under light-limited conditions below the canopy, must have affected photosynthesis. Because of this, growth was slow and seedlings could not easily replace dead or abscised leaves. Although insect defoliation was also observed in seedlings of *M. lutea*, no mortality occurred. This indicates that the damage was light. Pioneer species are known to be more susceptible to herbivores and pathogens (Coley, 1983a & b; Bazzaz, 1984; Dirzo, 1984) because they have less tough leaves, lower concentration of phenolics, and have higher nitrogen and water contents (Coley, 1983b).

Seedling mortality in *C. africana* and *V. keniensis* was also possibly caused by fungal pathogens. According to Augspurger (1983 and 1984) fungal diseases can be a major source of seedling mortality under heavy shade. In the present study, it was difficult to determine whether the seedlings died as a result of fungal attack. However, since seedlings of *C. africana* and *V. keniensis* had been weakened by combined effects of low irradiance and insect defoliation, they were more vulnerable to fungal attack. Seedlings of pioneer species are also known to show higher mortality due to fungal diseases than those of shade tolerant species (Augspurger, 1984). Since seedlings of the other species, *M. lutea* and *O. capensis*, showed almost no mortality under the heavy shade, they were probably unaffected by fungal pathogens.

The increase in seedling mortality rate in *V. keniensis* about 7 months after planting coincided with the start of the dry season. This suggests that the drought, and probably competition from the canopy trees, might have also contributed to seedling mortality in *C. africana* and *V. keniensis.* However, since mortality in these species also occurred during the rainy season, for example in November (Figure 7.3), drought was, therefore, not a major factor. At the time of harvesting the seedlings, the roots of the canopy trees had not grown in to the rooting zones of the seedlings, indicating that direct root competition from the canopy trees was also probably less important.

Given the observed trends in survival or mortality of the four species, it is clear that seedlings of *M. lutea* and *O. capensis* would have persisted under the heavy shade for a longer time. However seedlings of *C. africana* and *V. keniensis* were unlikely to survive the following season when the upper canopy trees came into full leaf.

Shade tolerance is a major criterion in most ecological classifications of tropical forest tree species (Popma and Bonger, 1988). Augspurger (1984) used survival rate of seedlings in shade as an index for shade tolerance. According to this criterion, seedlings of *O. capensis* and *M. lutea* appear to be shade-tolerant, while those of *C. africana* and *V. keniensis* are not. Because it had moderate survival, *V. keniensis* appeared more shade-tolerant than *C. africana,* suggesting that *V. keniensis* is more of a medium size gap species.

The results of survival rates of seedlings of *C. africana* and *V. keniensis* seem to be consistent with observations of Kigomo (1987). He recorded low and moderate survivals in seedlings/saplings of *C. africana* and *V. keniensis* respectively under enrichment planting. The high survival rates of seedlings of *O. capensis* and *M. lutea*, however, sharply contrasted with the same observations by this author who found low survival in both species. However, it is likely that seedlings in his studies were affected by antelope browsing. Parry (1957) reported that seedlings of *O. capensis* show high mortality beneath a forest canopy during the dry season. In the present study, the species showed no seedling mortality although there was a five-month dry season (Figure 7.2). The survival rates of seedlings of *C. africana* and *V. keniensis* on one hand, and those of *O. capensis* and *M. lutea* on the other hand, are consistent with the previous report of Fetcher *et al* (1983). They found that seedlings of a pioneer species, *H. appendiculatus,* showed survival of 49% while those of a shade-tolerant species, *D. panamensis,* had 100% survival under full shade (2% of full sunlight).

Height growth of seedlings was less marked at the beginning of the experiment although it was wet and the irradiance level was not very low, since the canopy species was not in full leaf. Seedlings were, therefore, slow in acclimating to the deep shade. For *C. africana* and *V. keniensis*, this observation is in agreement with that made in Chapter 4, in which seedlings of these species responded slowly after a decrease in irradiance. In Chapter 4, seedlings of *C. africana* and *V. keniensis* transferred from full sunlight to irradiance levels of 13-35% of full sunlight showed low and negative biomass RGR. Since the irradiance decreased to about 1.5% of full sunlight or less within two months after planting (when the canopy trees were in full leaf), the RGR in *C. africana* and *V. keniensis* must have been negative and the light level in the deep shade below the light compensation points of these two pioneer or gap species. It also seems that the RGR in *M. lutea* and *O. capensis* was low or negative because they also showed slow growth in height.

The dry matter production was highest in *M. lutea* possibly because its seedlings had more foliage. At seedling stage, the compound leaves of this species has 6-8 leaflets. Although *O. capensis* had more leaves than *M. lutea* (Table 7.2 and Figure 7.6), the latter had 56-76 leaflets per seedling. The size of a leaflet of *M. lutea* was about the same as that of a single leaf of *O. capensis.* The leaf area per seedling was therefore about four times greater in *M. lutea* than in *O. capensis.* Seedlings of *M. lutea,* therefore, had higher chances of benefiting from sunflecks than those of *O. capensis*, or the other two species which had fewer leaves. Although slow, height growth in *C. africana* and *M. lutea* continued throughout the duration of the experiment, indicating that soil moisture was probably not a limiting factor. The moderate R:FR ratio under the canopy did not result in etiolation in seedlings of these species. In both species, growth in height was more rapid after 12 months as indicated by the steep slope of the curves (Figure7.4). This was as a result of increased availability of light since the canopy trees were almost leafless at that time. It was also possibly due to increased moisture during the rains of November/December 1993 (Figure7.2). This, however, shows that despite the long period of suppression for a year, seedlings of these species were able to respond rapidly to increased availability of light and moisture. Pioneer species are known to respond rapidly to changes in resource levels (Bazzaz,1984 and1991). *C. africana* also showed a rapid response to changes in light availability in Chapter 4. The survival and growth of *C. africana* in this study were generally in agreement with that reported on seedlings of a pioneer species, *H. appendiculatus,* grown in deep shade of 2% of full sunlight (Fetcher *et al,* 1983). This suggests that under brighter light conditions, *C. africana* and *M. lutea* would have shown faster growth, and the survival of *C. africana* would have been probably better. *M. lutea* is associated with forest edges (Dale and Greenway, 1961; Eggeling and Dale, 1961). It is commonly planted in open areas in Western Kenya, and has long been regarded as a strong light demander. The present results, and those of the previous chapter, however, suggest that *M. lutea* is a moderately shade tolerant species, and capable of growing on a broader range of irradiance levels. Thompson *et al,* (1988) and Sharew (1994) have reported a similar observations in seedlings of *F. brayleyana* and *Juniperus procera* respectively.

Height and dry weight production in seedlings of *O. capensis* were moderate. Towards the end of the experiment, this species did not show a rapid growth in height in response to changes in resource levels (moisture and light) compared to *M. lutea* and *C. africana.* Instead, *O. capensis* produced more leaves (Figure 7.6) indicating that it invested a greater proportion of its assimilates in leaf production. This was possibly necessary to increase total leaf area per seedling and hence increase the chances of trapping sunflecks under low light, particularly when the canopy trees were in full leaf. Since this species regenerates under the plantations of *V. keniensis,* its high survival was not unexpected. However, its rate of growth was lower than expected. The results, however, show that *O. capensis* was the most shade tolerant among the four species. This confirms the observation made in the previous study (Chapter 6).

Growth (in height increment and dry matter production) was significantly lower in seedlings of *V. keniensis* than in those of the other species. This was in contrast to the results of the previous experiment (Chapter 6), in which *V. keniensis* grew faster than any other species. There are two possible reasons for the poor growth of this species under heavy shade. First, seedlings of *V. keniensis* were more severely defoliated by insects than those of the other species. This was because the same insects fed on the upper canopy trees and seemed to be host-specific. The tender leaves in seedlings were, therefore, likely to be more attractive to them than the mature trees. Secondly, seedlings of this species were planted under its own canopy. Augspurger and Kelly (1984) have reported that seedlings are more vulnerable to diseases when established around their parent trees than around the other species. Seedlings of *V. keniensis* might have, therefore, suffered more damage by fungal pathogens than those of the other species. The combined effects of damage by the insects and fungal pathogens seems to have resulted in net leaf losses and reduced growth. They also seem to have reduced the ability of seedlings to respond rapidly to increase in light and moisture like those of *C. africana* and *M. lutea* as discussed above. However, the fact that this species had moderately high survival of 68% under these conditions is an indication that it could have survived much better had its seedlings been planted under the canopy of another species.

7.5 CONCLUSIONS

Seedlings of *O. capensis* and *M. lutea* were able to survive and grow in deep shade for about 15 months and seem to be shade-tolerant. Seedlings of *C. africana*, in contrast, showed high mortality, while those of *V. keniensis* grew poorly. These two species are therefore shade-intolerant. Environmental conditions under young plantations of *V. keniensis* were suitable for regeneration of shade-tolerant species, as observed in the present study with *O. capensis* and *M. lutea*. *V. keniensis* can, therefore, be used as a nurse tree for the establishment of suitable shade-tolerant species. Seedlings of *M. lutea* can tolerate deep shade, but also seem to grow well under full sunlight.

CHAPTER 8

GENERAL DISCUSSION

8.1 INTRODUCTION

This study was carried out to obtain better understanding of the role of light and shade in the regeneration of *C. africana, V. keniensis, M. lutea* and *O. capensis.* The study was carried out under nursery and field conditions. The nursery experiments proved useful in understanding the responses of seedlings in the field. The results are in general agreement with the findings of other workers on responses of tropical tree seedlings to light environment. The results of the experiments have been discussed in detail and conclusions drawn in the relevant chapters. In the present chapter, the results are summarised and discussed in relation to responses of seedlings to shade, full sunlight, light quality and changes in the light environments. Implications of the findings for forest management are discussed and suggestions are made for future studies.

8.2 EFFECTS OF SHADE

The responses of seedlings to different levels of shade were determined in the nursery, a forest clearing and below a closed forest canopy. The light level under the forest shade was 1.5% of full sunlight, but varied from 16 to 61% of full sunlight in the nursery and in the forest clearing. The irradiance levels in the shaded treatments in the nursery and in the clearing were, therefore, relatively higher than that under the forest canopy. Due to unavailability of the right material, it was not possible to obtain lower irradiance levels (comparable to that below the canopy) in experiments carried out in the nursery and the forest clearing. Nevertheless, the levels of irradiance under the shaded treatments in the nursery and the clearing simulated light conditions in medium size to large canopy gaps, which are common in most of the logged tropical forests. The experiment beneath the canopy was carried out in a plantation. This demonstrated that the light level in the plantation was comparable to that beneath the understorey of a closed natural forest. However, there was no undergrowth in the plantation as is often the case on the forest floor of natural forests.

For a species to regenerate successfully in closed forest, its seedlings must persist for long periods under the deep shade. In the experiment carried out in the forest, seedlings of *C. africana* and *V. keniensis* showed high mortality. No mortality was, however, observed in any of the seedlings of these species grown under irradiance levels of 16-19% of full sunlight in the nursery and the clearing. Under the deep canopy shade, it was also clear that seedlings of these species were more susceptible to attacks by insect herbivores and fungal diseases. High humidity below the canopy, as indicated by the experiment carried out in the forest, is conducive to the spread of fungal diseases. Leaves of pioneer or gap species are also known to contain high levels of nitrogen (Coley, 1983b; Bazzaz, 1991) making the plants more palatable to the browsers. The seedlings planted under the canopy were protected and suffered limited browsing from small animals. This is not likely to be the case in natural forests where there are many browsers. For these reasons, successful regeneration of the two species is unlikely under closed forest canopies. However, their seedlings should survive in medium size forest gaps. Since such gaps are rare in less disturbed forests the occurrence of *C. africana* and *V. keniensis* should be localised. Being pioneer or gap species the seed dormancy displayed by these species should be light-regulated and any of their seeds dispersed into closed forests are unlikely to germinate, but will form seed-banks and wait for creation of a gap.

Seedlings of *M. lutea* and *O. capensis* persisted below the canopy for 15 months. Lack of competition from the undergrowth and good protection from browsing animals partly contributed to this high survival. Although this suggests that the results may not be extrapolated to natural forests where these factors are likely to influence survival, it is clear that planted seedlings of these species are capable of tolerating deep shade in the forest. While seeds of *O. capensis* do germinate below the mother trees in the forest, the wind-dispersed seeds of *M. lutea* probably do not germinate in deep shade. The shade tolerance displayed by *M. lutea* was not anticipated as the species is commonly grown in open areas. This finding should, therefore, be confirmed through nursery experiments. The high survival of *O. capensis* confirms that this species can invade the plantations of *V. keniensis* if seed trees are close by and adequate protection is provided. Since the regeneration of this species is usually poor under natural forests, this suggests that it benefits from the canopy of a deciduous species. *V. keniensis* can, therefore, be used as a nurse to regenerate *O. capensis.* Other species such as *P. africana*, *F. macrophylla* and *X. monospora*, which regenerate under the plantations of *V. keniensis* in Chuka forest, also seem to require nurse trees to establish well. In enrichment planting or other types of planting programme *V. keniensis* could therefore be a useful nurse tree.

Growth of all the species was slow under the forest canopy, but was faster under the dense shade (16% of full sunlight) in the clearing. *O. capensis, M. lutea, C. africana* and *V. keniensis* produced up to 5, 8, 20, and 160 times greater dry matter respectively, when grown under the dense shade treatment in the clearing than in the forest canopy. The four species, therefore, grow faster in medium size gaps than in small forest gaps. It is also clear that seedlings of these species would have grown faster if they had been planted in more open areas of the plantation.

In the nursery experiment, seedlings of *C. africana* and *V. keniensis* maintained positive values of RGR under irradiance level of 19% of full sunlight. However, their light compensation points were not determined and this needs to be done because of the importance of these species in reforestation programmes. The light levels under moderately shaded treatments in the nursery and the clearing were comparable. In the nursery, growth of seedlings of *C. africana* and *V. keniensis* was faster under moderate shade than under dense shade. These species will, therefore, grow faster in large canopy gaps than in medium size gaps. *V. keniensis* also grew faster under moderate shade in the clearing but the response of *C. africana* was disappointing. There is evidence that the poor growth of *C. africana* in the clearing was due to the low nutrient status of the soils. In the nursery, growth of both species was lower in seedlings raised under low nutrient regime than in those grown under high nutrient treatment. The response to increase in nutrient supply was more pronounced in seedlings of *C. africana* than in those of *V. keniensis*, especially in dry weight production. It is known that high nutrient supply lifts the nitrogen status of the leaves regardless of irradiance levels and this enhances photosynthetic processes (Thompson *et al,* 1988). Since the clearing had been subjected to continuous grazing (through cut and carry system), the soils must have been depleted of nutrients. This resulted in lower levels of leaf nitrogen and hence lower photosynthetic rate of seedlings. The response of seedlings of *C. africana*, shows that this species ought to occur in more fertile sites, and its regeneration will be limited in nutrient-poor soils. In newly formed canopy gaps both species are likely to benefit from the flush of nutrients. However, canopy gaps are heterogeneous (Hartshorn, 1980). Soil nutrients are likely to be higher in zones around the roots and in areas covered by the decaying leaves. The two species are, therefore, likely to colonise different zones in a gap. While regeneration of *V. keniensis* is likely to succeed in most parts of the gap, that of *C. africana* will be restricted to zones endowed with nutrients. Similarly, the latter will require more fertile sites if used in enrichment planting in large canopy gaps.

8.3 RESPONSES TO FULL SUNLIGHT

It has been widely reported that drastic canopy opening, caused by logging or forest clearing, results in increased light levels, temperatures, vapour pressure deficits (Fetcher *et a*l, 1985; Whitmore, 1985; Eamus *et al* 1990) and changes in soil nutrients (Jordan, 1991). It is known that such changes have adverse effects on survival or growth of seedlings of certain species (Eamus *et al,* 1990). One of the aims of this study was to examine the effects of full sunlight on growth of seedlings of some important tree species in Kenya. The study has shown that the highest levels of light, temperatures and vapour pressure deficits observed under full sunlight, were consistent with the previous reports. The study has also shown that seedling survival was not affected by full sunlight in the clearing. However, full sunlight depressed height growth in three out of the four species studied in the clearing (Chapter 6). In the nursery, the responses of seedlings of the main study species (*C. africana* and *V. keniensis*) to full sunlight were affected by the supply of nutrients (Chapter 3).

In the nursery, the growth of *C. africana* was relatively faster than that of *V. keniensis*; indicating that the former is more light demanding. Low supply of nutrients enhanced the RGR and dry weight production in *C. africana*, but depressed them in *V. keniensis*. Leaves of seedlings grown at high irradiance are generally thicker with more mesophyll, higher stomatal conductance and higher maximal rates of photosynthesis (Sinclair, 1977; Mooney, 1986; Thompson *et al* 1988). In this study seedlings of both species grown under full sunlight had thicker leaf lamina (lower specific leaf area) than those grown in shade. This must have enhanced the photosynthetic rates in seedlings of *C. africana*. However, low nutrients seem to have limited the response in seedlings of *V. keniensis.*

Thompson *et al* (1988) have shown that leaves of seedlings grown in high nutrients have higher levels of leaf nitrogen, and hence the carboxylating enzyme, ribulose biphosphate carboxylase oxygenase (RUBISCO). Higher concentration of the carboxylating enzyme enhances the photosynthetic capacity of the leaves (Thompson *et al,* 1988; Riddoch *et al*, 1991). Under full sunlight in the nursery high supply of nutrients enhanced the NAR, RGR, biomass production and growth in height in seedlings of *V. keniensis*, but depressed in those of *C. africana.* Seedlings of *V. keniensis,* probably responded to enhanced levels of the carboxylating enzyme by increasing their photosynthetic rates under full sunlight. In contrast, the RGR of seedlings *C. africana* declined. There was evidence that the growth of this species was limited by water supply, which resulted in stomatal closure.

In the clearing, dry weight production and height growth were depressed by full sunlight in seedlings of *M. lutea, O. capensis* and *V. keniensis*. In contrast, *C. africana* showed higher growth in height and biomass production under full sunlight. There was evidence that the soils in the clearing were low in nutrients. This probably lowered the level of leaf nitrogen and the carboxylating enzyme resulting in low photosynthetic capacity of the leaves in seedlings of *M. lutea, O. capensis* and *V. keniensis*. Thompson *et al* (1988) and Kamaluddin (1991) have reported depressed growth in seedlings grown under a combination of low nutrients and high irradiance. Seedlings of *M. lutea, O. capensis* and *V. keniensis* could have also suffered photoinhibition resulting in retarded growth. According to Langenheim *et al* (1984), the rates of photosynthesis sometimes decline under high irradiance because of photoinhibition. Although this could be closely linked to stomatal closure, it is possible that the terminal meristems of these less light demanding species might have been damaged by high irradiance, resulting in increased branching under full sunlight. Availability of soil moisture also confounded the effects of high irradiance. The high evapotranspirational losses associated with the clearings probably induced stomatal closure and decreased rates of photosynthesis much earlier in the day in these less light demanding species. This would be followed by reduced nutrient uptake from the soil. Under such circumstances the pattern of allocation of assimilates also changed in favour of roots to enhance survival, which became more critical.

Abandoned clearings in tropical forest lands are generally poor in soil nutrients. Soil moisture is also critical in seedling survival, especially during the dry seasons. Selection of tree species for such sites should, therefore, take into account their nutritional requirements. The role of mycorrhiza may be important in enhancing nutrient uptake as well.

8.4 EFFECTS OF LIGHT QUALITY

The main effect of reduction in R:FR ratio was the increase in stem elongation in seedlings of *C. africana* and *V. keniensis*. However, this was only observed under extremely low R:FR ratio of 0.02. Under medium R:FR ratios of 0.36 and 0.65, stem elongation was not observed. Stem extension under very low R:FR ratio was accompanied by a shift in biomass allocation from roots to the stem. The mechanism of stem extension in plants is related to a photoreceptor (phytochrome), which operates through photoequilibrium to perceive the relative amounts of red and far-red light (Smith, 1981a). Low R:FR ratios strongly reduce phytochrome photoequilibrium, and a negative linear relationship has been found to exist between the photoequilibrium and stem elongation rate (Morgan and Smith, 1981; Smith, 1982). Warrington *et al* (1988) have also found that a reduction in photoequilibrium resulted in increased stem extension in a pioneer species, *Pinus radiata*.

Several studies have shown that seedlings of pioneer tropical forest trees show greater stem elongation compared to those of shade tolerant species (Kwesiga and Grace, 1986; Kamaluddin, 1991). In this study, the pioneer species, *C. africana*, did not show marked stem elongation as expected. Moreover, it was even less sensitive to changes in R:FR ratio compared to the gap species, *V. keniensis*. Since *C. africana* is a widely distributed species, it is possible that variation exists within the species. Trees which grow in open areas usually have poor stem form, while those growing in the forest may have straight boles (Mihretu, 1994). It also appears that this species may show some response to reduced R:FR ratio in some aspects of its growth. It has been shown that reduced R:FR ratio enhances apical dominance (Warrington *et al,* 1988), and conversely, high R:FR ratio should weaken apical dominance. A typical tree of *C. africana* growing in the open is usually heavily branched and the crown lacks a leading shoot. This is possibly due to high R:FR ratio. In an openly growing tree, a branch or a new stem may occasionally develop from the base. Under the existing shade, the new stem grows rapidly with a straight bole and may eventually become the leading shoot. However, as soon as it emerges above its own crown the new leader begins to branch. This is possibly caused by high R:FR, suggesting that *C. africana* may respond to reduced R:FR ratio in canopy gaps.

Although seedlings of *V. keniensis* did not show a marked response to medium R:FR ratio in the nursery and below the forest canopy, seedlings in the clearing showed elongated shoots (under R:FR ratio of 0.88). There are two possible reasons to explain this. First, the seeds used came from two different sources and there could be within-species variation. Any such variation is, however, likely to be small because *V. keniensis* occurs in a restricted range around Mt. Kenya. Secondly, it has been shown in Chapters 3 to 5 that this species shows initial slow growth under nursery conditions. It is, therefore, probable that the response will be different once the seedlings are established in the field, especially under medium size canopy gaps.

8.5 ACCLIMATION TO SUDDEN CHANGE IN THE LIGHT ENVIRONMENT

The ability of seedlings of a given species to survive and grow in response to sudden change in light environment depends on their capacity to adjust or acclimate in terms of their physiology and morphology. This study has shown that seedlings of *C. africana* and *V. keniensis* had similar acclimation potential and their adjustment to change in light environment was complete within a month. The effects of the previous light regimes influenced the adjustment, and acclimation to increase in light availability was faster than acclimation to decrease. It was also observed that although acclimation to change in light environment was mainly physiological, shifts in biomass allocation pattern was in favour of shoots and roots when seedlings were shaded and exposed respectively. It was also shown that the supply of nutrients did not influence the acclimation potential of the seedlings.

In seedlings which were exposed after growing under irradiance level of 12% of full sunlight and low R:FR of 0.02, severe leaf scorching was observed and this resulted in 25-50% seedling mortality. No mortality was observed in seedlings previously grown under irradiance levels of 19-52% of full sunlight, although leaf scorching occurred at varying levels. Severe bleaching/scorching of the leaves in seedlings transferred from low to high irradiance or full sunlight has been attributed to photoinhibition and lethal leaf temperatures (Turner and Newton, 1990; Kamaluddin and Grace, 1992a). In this study, leaves of seedlings which had been grown under 12% of full sunlight were considerably thinner (higher specific leaf area) than those previously under 19-52% full sunlight. Also, shade leaves have low levels of carboxylating enzyme (Mooney, 1986) and the high energy trapped cannot be fully used resulting in photoinhibition. Since seedlings also experienced higher temperatures and saturation deficits following exposure, it is clear that the effects of sudden increase in light levels were due to combination of these factors, resulting in seedling mortality. These findings show that seedlings of *C. africana* and *V. keniensis*, growing in dense shade with irradiance levels of about 12% of full sunlight would be severely damaged by sudden occurrence of a gap or clearing. Also, heavily shaded nursery seedlings will show high mortality or checked growth if suddenly planted in open areas.

The effects of exposure of seedlings of *M. lutea* and *O. capensis* was not investigated. However, because these species were more shade tolerant than either *C. africana* or *V. keniensis* (Chapters 6 and 7), seedlings of *M. lutea* and *O. capensis* are expected to show high mortality if suddenly exposed to full sunlight.

Growth was reduced in seedlings of *C. africana* and *V. keniensis* which were transferred from full sunlight to dense shade (13% of full sunlight). Seedlings transferred from moderate shade (44 and 52% of full sunlight) to dense shade (13% of full sun light) also showed similar response. Leaves become thicker when seedlings are transferred from low to high irradiance and this is associated with thicker palisade and mesophyll tissues (Thompson *et al* 1988; Kamaluddin and Grace, 1993). Such leaves have a higher number of chloroplasts per unit leaf area and this enhances the amount of carboxylating enzyme and hence the photosynthetic capacity of the leaves (Sinclair *et al*, 1977; Thompson *et al*, 1988; Kamaluddin and Grace, 1993). In this study, seedlings transferred from shade to full sunlight developed thicker leaves and this seems to have enhanced the capacity of seedlings to photosynthesise as reflected by higher NAR, RGR and biomass production. On the other hand, seedlings transferred from full sunlight to shaded environment developed thinner leaves (high specific leaf area). These leaves may have had lower levels of carboxylating enzyme, which limited their photosynthetic rates, resulting in low NAR. Although, the LAR increased in seedlings transferred from full sunlight to shade, this did not compensate for the low NAR and, as a result the RGR remained low and sometimes negative. Acclimation to change in light availability was, therefore, mainly physiological. These observations suggest that growth will be checked when seedlings raised in the open conditions in the nursery are planted in small gaps in the forest. The findings were confirmed by the experiment carried out beneath the forest canopy (Chapter 7).

High irradiance leads to greater nitrogen contents compared with shade-grown material when nutrient availability is high (Björkman 1981). In this study, the supply of nutrients had no significant influence on the capacity of seedlings to acclimate. This was not expected. However, since the supply of nutrients at high level tended to enhance the acclimation potential of seedlings of *C. africana*, it is possible that the effects of nutrients could have been different if the experiment had continued for a longer time. These results suggest that adjustment of seedlings of *C. africana* and *V. keniensis* to sudden canopy opening will not be affected by the nutritional status of the soils.

8.6 ADAPTATION TO SHADE AND FULL SUNLIGHT

Seedlings of *C. africana* and *V. keniensis* adapted to shade by increasing allocation of assimilates from the roots to stem and leaves. Since the leaf weight ratio was unaffected by irradiance, increased allocation of assimilates from the roots actually went into stem growth. It was observed in Chapter 5 that the specific stem length increased under low R:FR ratio and that seedlings also shifted allocation of biomass from the roots to the stems. It would appear, therefore, that under shaded conditions, increased biomass allocation to the stems was a response to reduced R:FR ratio. Warrington *et al* (1988) suggested that a pioneer species, *P. radiata*, had evolved phytochrome-related mechanisms to detect changes in the R:FR ratio under plant canopies, and these mechanisms enable the plants to alter their growth responses to effectively compete against neighbouring plants. Since both *C. africana* and *V. keniensis* are associated with large forest gaps or clearings, their adaptation to shade seems to be related to the light quality.

Shade-grown seedlings of *C. africana* and *V. keniensis* had thinner leaves (high specific leaf area) with flat laminae. It seems that shading results in redistribution of biomass within the leaves to increase the leaf area and enhance light interception under low irradiance. Under shade in the nursery and in the field, seedlings of these species showed increased leaf abscission. This was probably a strategy to maintain carbon balance by reducing the number of leaves, especially those photosynthetically less efficient. Beneath the canopy, seedlings of fairly shade-tolerant *O. capensis* and *M. lutea* did not shed their leaves, as they needed larger area of leaves to intercept available light under very low irradiance.

Leaves of seedlings of *C. africana* and *V. keniensis* grown in full sunlight had lower specific leaf area (SLA) and, therefore, had thicker laminae compared to leaves of seedlings grown in the shade. In seedlings transferred from shade to full sunlight, re-orientation of leaf laminae from horizontal to v-shaped position was an adaptation to minimise the direct effects of radiation. The thicker leaves also reduced light transmission. Root weight ratio was also higher in seedlings of both species grown under full sunlight and, in those grown at low level of nutrients supply. Increase in root weight ratio was due to a shift in pattern of assimilate allocation from shoot (mainly stems) to roots. This is usually one of the mechanisms under which plants adapt to soil drying (Osonubi and Davies, 1981; Molyneux and Davies, 1983; Khalil and Grace, 1992) and reduced nutrient status of the soils (Chapin, 1980). Increased allocation of assimilates to roots will stimulate the growth of roots and thereby ensure effective use of water and nutrients in the deeper soil profile.

Seedlings planted in the clearing in full sunlight, had lower height increment and were more branchy. This could be due to the effects of high R:FR (1.10) ratio which depressed the growth of terminal shoot and thereby encouraging increased branching. It is also possible that by reducing apical dominance, high R:FR ratio stimulates the growth of roots and this may be one of the mechanisms involved in increased allocation of assimilates to the roots in sun-grown plants

8.7 IMPLICATIONS FOR FOREST MANAGEMENT

8.7.1 Natural Forest Management

The selective cutting system has been practised in Kenya for many years. Because there has been little control over it, this has resulted in varying cutting intensities depending largely on the distribution and stocking of the commercial or desired species. Many forests are, therefore, characterised by the presence of numerous gaps and clearings of different sizes. These gaps have been invaded by fast growing pioneer weedy species, which have retarded the regeneration of the valuable species. This study has shown that *V. keniensis, O. capensis, M. lutea*, and to some extent *C. africana,* are adapted to conditions in canopy gaps. A selective felling system will, therefore, favour the regeneration of these species. However, other factors may limit their regeneration, and availability of seeds is probably the most important. Where cutting has depleted mother trees, regeneration will rely on seed dispersal from outside and this is likely to slow down the rate of forest recovery. Selective felling should, therefore, ensure that mother trees of superior quality are retained. Because the gaps have been colonised by rapidly growing pioneer species, regeneration of the desired or overcut species will occur later in the succession, even when the seeds are available. This may take several decades. Where forest policies require accelerated recovery of degraded forests, silvicultural interventions will be necessary. This can be achieved through enrichment planting. However, because of the presence of many weedy species, measures to increase the competitive ability of planted seedlings should be considered in such programmes. This may include the use of large planting stock to ensure that seedlings are not heavily shaded. Moderately shade/light demanding species, as shown in this study, will also be adversely affected by full sunlight. The size of planting stock should, therefore, aim at maintaining moderate shading levels, especially in large gaps.

In newly formed gaps or in areas that will be brought under selection felling system in future, timely planting is likely to result in more successful establishment of seedlings. Group planting will increase the chances of success, particularly where weeds and browsing are likely to be major problems. As shown in this study, canopy species such as *V. keniensis*, can create conditions favourable for the regeneration of more shade tolerant species. For this reason, enrichment planting should not, in the long run, result in reduction in species diversity, provided that seed trees of diverse shade-tolerant species are available.

It has been shown in this study that the supply of nutrients at high level enhanced the growth of *C. africana* and *V. keniensis*. In a recent similar study, Sharew (1994) has also found the same results in *Juniperus procera* (cedar) and *Afrocarpus gracilior* (podo). These are also some of the most valuable timber trees in Kenya. It is, therefore, evident that the supply of nutrients has an important influence in the regeneration of indigenous tree species in Kenya. This implies that during logging, it is necessary to minimise soil disturbance. It also suggests that in enrichment planting, the siting of a species in the opening is important, since soil fertility will vary within the gap.

Although enrichment planting is necessary to accelerate recovery of degraded forests, it is likely to be more expensive than natural regeneration. For this reason, natural regeneration will still be necessary. This study has shown that *O. capensis* can regenerate in medium size gaps, receiving light levels of about 40% of full sunlight. Selection felling that will result in light gaps will favour the regeneration of this species. It is, therefore, possible to encourage natural regeneration of this species and others, which seem to have the same light requirements such as *Prunus africana* and *Fagara macrophylla.* Where advance regeneration is present, it may be necessary to gradually reduce the canopy to avoid sudden release, which is most likely to result in high mortality as observed in this study.

8.7.2 Plantation Management

One of the common features of forests in Kenya, and probably in many other tropical countries, is the presence of large abandoned clearings. Because such areas had been cultivated previously, they are generally poor in soil nutrients. Such clearings need to be brought under forest cover for productive and protective purposes, and planting of indigenous tree species is likely to be given preference. Results of this study have shown that *C. africana* is suitable for planting under full sunlight. Growth in height was depressed under full sunlight in *V. keniensis* and was highest under moderate shade. Under full sunlight, this species will also be branchy. This species has been successfully cultivated as one of the major hardwoods in the country. Although the initial heavy branching will be reduced as the canopy of the trees close due to mutual shading, it is doubtful if the trees ever regain the initial loss in height growth. This is supported by the fact that under moderate shade the height growth of seedlings was almost twice that of their counterparts grown under full sunlight. The stem quality may not improve also due to inital heavy branching. It might, therefore, be advisable to establish this species under a nurse tree, probably *Grevillea robusta.* This should be tested under field conditions.

Growth of *C. africana* and *V. keniensis* was enhanced by the supply of nutrients at high level. In *C. africana*, growth declined under full sunlight because of inadequate supply of moisture. In clearings, survival of seedlings will be critical during the dry season. It will, therefore, be necessary to match the species according to their requirements for water and nutrients. In high rainfall areas, for example, the potentials of *C. africana* and *V. keniensis* will be realised in fertile soils. In low rainfall areas, the growth will be limited by soil moisture even when the soils are fertile. Cultural measures that will result in conservation of moisture, such as weeding may improve the uptake of nutrients, but this might be over a limited period. Under moderate shade and weed free conditions in early years, the growth of *V. keniensis* is comparable to that of the main exotic species, *Pinus patula* and *Cupressus lusitanica,* in Kenya. Where there is a need to establish *O. capensis* in plantations it should be planted under a nurse crop. However, *M. lutea* is suitable for plantation establishment without a nurse crop.

8.7.3 Agroforestry Systems

In Kenya, *C. africana* has been used in agroforestry systems as a shade tree for agricultural crops such as coffee and bananas. It is also a popular shade tree in homesteads and pasture lands. In this study, it has been shown that its growth is enhanced by the supply of nutrients at high level and that it is sensitive to moisture stress. It also shows a high leaf turn-over. The results suggest that *C. africana* is both nutrient and water demanding. When used in agroforestry systems, it is probably a strong competitor for water and nutrients. However, its effects are unlikely to be noticed, because crops grown with it usually receive regular amounts of inorganic fertilisers. Although it shows high leaf turn-over, this is only likely to be realised in fertile sites in high rainfall areas. For this reason its use as agroforestry species should be limited to moist areas, where heavy leaf shedding will provide useful mulch in soil conservation.

8.8 EXPERIMENTAL LIMITATIONS

This study was undertaken to determine the responses of seedlings to different levels irradiance, light quality and changes in the light availability. Artificial shading was used in the experiments carried out in the nursery and the clearing. The light environment was, therefore, different from that under vegetational shade in spectral composition. Although the light environment beneath the plantation simulated that on the forest floor of a natural forest, the undergrowth was lacking. In the nursery and the clearing, the shade-houses were small and shading of smaller seedlings by the larger ones must have occurred in the mornings and in the evenings on sunny days. This, however, depended on the location of seedlings within the shade-houses. This was minimised by regular relocation of seedlings in the nursery. In the nursery, the watering system resulted in supplying probably similar amounts of water to small and the large seedlings. Larger seedlings, therefore, probably received a relatively less amount of water. In the light quality experiment, the neutral filter did not function as expected and, therefore, the effects of low and high R:FR ratios could not be compared. In the clearing, soil fertility was quite variable and this influenced the response of some species. The site selected was the only one available where there was little interference from the elephants. Among the four study species, the responses of *M. lutea* and *O. capensis* were not determined in the nursery. This was mainly due to inadequate space in the shade-houses. In spite of these limitations, the results obtained are consistent with previous studies on responses of tropical tree seedling to different light environments. This study has, therefore, been largely successful.

8.9 FURTHER WORK

The study was carried out to generate information for improved silvicultural management of indigenous tree species in Kenya. The results obtained from the study should, therefore, be tested under the field conditions. In particular, the enrichment planting of *O. capensis* and *V. keniensis* should be tried in medium size and large gaps respectively. *V. keniensis* should also be planted under a nurse tree, e.g., *Grevillea robusta* to test its performance.

This study examined the responses of seedlings to different levels of light, but did not determine the rates of photosynthesis. It would be useful to investigate this in relation to water and nutrient supply. As observed in this study *C. africana* and *V. keniensis* had mycorrhizal roots, but investigations were not carried out on their possible influence on responses of seedlings to different levels of light. This should be determined in any future related studies.

Results from the experiment carried out beneath the forest canopy showed that *O. capensis* and *M. lutea* were fairly shade-tolerant. Investigations on these species and others such as *Prunus africana* and *Fagara macrophylla* should now be extended to natural forests. Future studies should be maintained until the plants have reached sapling stage. Since the response of *M. lutea* was contrary to the expectations, there is a need to confirm this through nursery studies.

Since the light levels vary considerably in time and space, it is necessary to determine the light levels received in various sizes of gaps in different times of the year. The success of natural regeneration depends, among other factors, on the availability of seed. This study showed that it might be possible to obtain advance regeneration in *O. capensis* in medium size canopy gaps. There is a need to undertake detailed studies on seed biology and any other factors which may influence natural regeneration in this species.

REFERENCES

Ahenda, J.O. (1991). Processing of pulpy seed. In: *1st National Tree Seed Workshop* (Ed. P. Schnier). KEFRI, Nairobi.

Amin, H.M. (1990). *Trees and Shrubs of the Sudan*. Itaca Press, Exeter.

Ampofo, S.T. and Lawson, G.W. (1972). Growth of seedlings of *Afrormosia elata.* Harms in relations to light intensity. *J. App. Ecol.* **9,** 301-306.

Augspurger, C.K. (1983). Seedling dispersal of tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. *J. Ecol.* **71**, 759-771.

Augspurger, C.K. (1984). Light requirements of neotropical tree seedlings: A comparative study of growth and survival. *J. Ecol.* **72,** 777-795.

Augspurger, C.K. and Kelly, C.K. (1984). Pathogen mortality of tropical tree seedlings: experimental studies of effects of dispersal, seedling density and light conditions. *Oecologia* (Berlin) **61**, 211- 217.

Battiscombe, E. (1936). *Trees and Shrubs of Kenya Colony.* Government Printer, Nairobi.

Bazzaz, F.N. (1984). Dynamics of wet tropical forests and their species strategies. In: *Physiological Ecology of Plants of Wet Tropics* (Eds. E. Medina, H.A. Mooney and C. Vanquez-Yanes). Junk, The Hague.

Bazzaz, F.N. (1991). Regeneration of tropical forests: physiological responses of pioneer and secondary species. In: *Rainforest Regeneration and Management* (Eds. A. Gomez-Pompa, T.C. Whitmore and M. Hadley), pp 91-117. UNESCO, Paris.

Bazzaz, F.N. and Pickett, S.T.A. (1980). Physiological ecology of tropical succession: A comparative review. *Ann. Rev. Ecol. Syst.* **11**, 287-310.

Bekele, A., Birnie, A. and Tengnas, B. (1993). *Useful Trees and Shrubs for Ethiopia.* Regional Soil Conservation Unit, SIDA, Embassy of Sweden, Nairobi.

Bengough, C.C. (1970). Kenya timbers suitable for furniture. *Timber Leaflet No. 10.* Kenya Litho Ltd., Nairobi.

Björkman, O. and Ludlow, M.M. (1972). Characteristics of light climate on the floor of a Queensland rainforest. *Carnegie Institution Year Book* **71**, 85-94.

Björkman, O. (1981). Responses to different quantum flux densities. In: *Encyclopaedia of Plant Physiology* (Eds. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler), pp 57-107. Springer-Verlag, Berlin.

Bongers, F., Popma, J. and Irriarte-Vivar, S. (1988). Response of *Cordia megalantha* Blake seedlings to gap environment in tropical rain forest. *Functional Ecol.* **2,** 379-390.

Brown. L.H. and Cocheme, J. (1969). *A study of the Agroclimatology of the Highlands of Eastern Africa*. FAO, Rome.

Burton, P.H. and Mueller-Dumbois, D. (1984). Response of *Metrosidoris polyorpha* seedlings to experimental canopy opening. *Ecology* **65**, 779-791.

Chapin, F.S. (1980). The mineral nutrition in plants. *Ann. Rev. Ecol. Syst.* **11,** 233 - 260.

Chazdon, R.L. and Fetcher, N. (1984a). Light environment of tropical forests. In: *Physiological Ecology of Plants of Wet Tropics* (Eds. E. Medina, H.A. Mooney and C. Vanquez-Yanes), pp 27-35. Junk, The Hague.

Chazdon, R.L. and Fetcher, N. (1984b). Photosynthetic light environment in a lowland tropical rain forest in Costa Rica. *J. Ecol.* **72,** 553-564.

Coley, P.D. (1983a). Intraspecific variation in herbivory on two tropical tree species. *Ecology* **64,** 426-433.

Coley, P.D. (1983b). Herbivory and defensive characteristics of tree species in lowland tropical forest. *Ecol. Monogr.* **53,** 209- 233 .

Coombe, D.E. (1960). An analysis of the growth of *Trema guineensis. Ecology* 48, 219-231

Corré, W.J. (1983a). Growth and morphogenesis of sun and shade plants I. The influence of light intensity. *Acta Bot. Neerl.* **32,** 49-62.

Corré, W.J. (1983b). Growth and morphogenesis of sun and shade plants II. The influence of light quality. *Acta Bot. Neerl.* **32**, 185-202.

Dale, I.R. and Greenway, P.J. (1961). *Kenya Trees and Shrubs*. Buchanan's Kenya Estates Ltd., Nairobi.

Denslow, J.S. (1980). Gap partitioning among tropical rainforest trees. *Biotropica* (Suppl.) **2,** 47-55.

Dirzo, R. (1984). Insect-plant interactions: some ecological consequences of herbivory. In: *Physiological Ecology of Plants of Wet Tropics* (Eds. E. Medina, H.A. Mooney and C. Vanquez-Yanes). Junk, The Hague.

Eamus, D., Lawson, G.J., Leakey, R.R.B. and Mason P.A. (1990). Enrichment planting in the Cameroun moist deciduous forest: microclimatic and physiological effects. *Proc. XIX World Forestry Congress* **1,** 258-270.

Eggeling, W.J. (1947). Working plan for the Budongo and Siba Forests, Uganda Forest Department. Government Printer, Entebbe.

Eggeling, J.W. and Dale, I.R. (1961). *The Indigenous Trees of Uganda Protectorate*. Government Printer, Entebbe.

Fetcher, N., Strain, B.R. and Oberbauer, S.F. (1983). Effect of light regime on growth, leaf, morphology and water relations of seedlings of two species of tropical trees. *Oecologia* (Berlin) **58,** 314-331.

Fetcher, N., Oberbauer, S.F. and Strain, B.R.(1985). Vegetation effects on microclimate in lowland tropical forest in Costa Rica. *International Journal of Biometeorology* **29**, 145-155.

Gomez-Pompa, A. and Burley, F.W. (1991). The management of natural tropical forests. In: *Rainforest Regeneration and Management* (Eds. A. Gomez-Pompa, T.C. Whitmore and M. Hadley), pp 3-18. UNESCO, Paris.

Herrera, H.R.A., Capote, R.P., Menendez, L. and Gunatilleke, I.A.U.N. (1991). Silvigenesis stages and the role of mycorrhiza in natural regeneration in Sierra Del Rosario, Cuba. In: *Rainforest Regeneration and Management* (Eds. A. Gomez-Pompa, T.C. Whitmore and M. Hadley), pp 211 -221. UNESCO, Paris.

Hartshorn, G.S. (1980). Neotropical forest dynamics. *Biotropica* (Suppl.) **12,** 23-30.

Hoad, S.P. and Leakey. R.R.B. (in press). Morphological and physiological factors induced by light quality and affecting rooting in *Eucalyptus grandis.*

Hunt, R. (1978). *Plant growth analysis*. Edward Arnold, London.

Huxley, P.A. (1967). The effects of artificial shading on some growth characteristics of Arabica and Robusta coffee seedlings I. The effect of shading on dry weight, leaf area and derived growth data. *J. App. Ecol.* **4,** 291-308.

Irvine, F.R. (1961). *Woody Plants of Ghana.* Oxford University Press, London.

Janos, P.J. (1983). Tropical mycorrhiza, nutrient cycles and plant growth. In: *Tropical Rain Forest Ecology and Management* (Eds. S.L. Sutton, T.C. Whitmore and A.C. Chadwick), pp 327-345. Blackwell Scientific Publications, Oxford.

Jordan, C.F. (1991). Nutrient cycling process and tropical forest management. In: *Rainforest Regeneration and Management* (Eds. A. Gomez-Pompa, T.C. Whitmore and M. Hadley), pp 159-180.

Kamaluddin, M. (1991). The growth and physiology of tropical forest tree seedlings in relation to light. PhD thesis, University of Edinburgh.

Kamaluddin, M. and Grace, J. (1992a). Photoinhibition and light acclimation in seedlings of *Bischofia javanica*, a tropical forest tree from Asia. *Annals of Botany* **69,** 47-52.

Kamaluddin, M. and Grace, J. (1992b). Acclimation in seedlings of a tropical tree, *Bischofia javanica*, following a stepwise reduction in light. *Annals of Botany*, **69**, 557-562.

Kamaluddin, M. and Grace, J. (1993). Growth and photosynthesis of tropical forest tree seedlings (*Bischofia javanica* Blume) as influenced by a change in light availability. *Tree Physiology* **13**, 189-201.

Kenya Forestry Department (1969). Treatment of *Vitex keniensis* plantations. *Technical Order No. 47.*

Kenya Government (1968). A Forest Policy for Kenya. *Sessional Paper No. 1 of 1968*. Government Printers, Nairobi.

Kenya Meteorological Department (1984). Climatological Statistics For Kenya, Nairobi.

Khalil, A.A.M. and Grace, J. (1992). Acclimation to drought in *Acer pseudoplatanus* L. (Sycamore) seedlings. *Journal of Experimental Botany* **43,** 1591-1602.

KIFCON (1994). Kenya indigenous forest conservation programme. *Phase1 Report,* Nairobi.

Kigomo, B.N. (1981). Observations on the growth of *Vitex keniensis* Turill (meru oak) in plantations. *E. Afr. Agri. For. J.* **47**, 32-37.

Kigomo, B.N. (1987). Some observations on regeneration trials in Kakamega and South Nandi natural forests, Kenya. *E. Afri. Agri. For. J.* **52**, 184-195.

Kigomo, B.N. (1989). Studies on the regeneration and growth characteristics of *Brachylaena huillensis* in semi-deciduous forests of Kenya. PhD thesis, University of Oxford.

Kigomo, B.N. (1990). Influence of shade on the growth of seedlings of *Brachylaena huillensis* in forest and nursery conditions. *E. Afr. Agri. For. J.* **56,** 27-36.

King, D.A. (1991). Correlation between biomass allocation, relative growth rate and light environment in tropical forest saplings. *Functional Ecol.* **5**, 485-492.

Kramer, P.J. and Kozolwski, T.T. (1960). *Physiology of Trees*. McGraw-Hill, New York.

Kriek, W. (1968). Report on species trials in *Celtis-Holoptelea* forest sites in East Mengo and Busoga. *Uganda Forest Department Tech. Note* No. 152.

Kwesiga, F.K. (1985). Aspects of the growth and physiology of tropical tree seedling in shade. PhD thesis, University of Edinburgh.

Kwesiga, F.K. and Grace, J. (1986). The role of the red/far-red ratio in response to tropical tree seedlings shade. *Annals of Botany* **57**, 283-290.

Kwesiga, F.R., Grace, J. and Sandford, A.P. (1986). Some photosynthetic characteristics of tropical timber trees as affected by the light regime during growth. *Annals of Botany* **58**, 23-32.

Langeheim, J.H., Osmond, C.B., Brooks, A. and Ferar, P.J. (1984). Photosynthetic responses to light in seedlings of selected Amazonian and Australian rain forest tree species. *Oecologia* (Berlin) 63, 215-224.

Lee, D.W. (1987). The spectral distribution of radiation in two neotropical forests. *Biotropica* **19**, 161-166.

Lee, D.W. (1988). Simulating forest shade to study the development ecology of tropical plants: juvenile growth in tree vines in India. *J. Trop. Ecol.* **4,** 281-292.

Lee, D.W. (1989). Canopy dynamics and light climates in a tropical moist deciduous forest in India. *J. Trop. Ecol.* **5,** 65-79.

Logie, J.P.W. and Dyson, W.G. (1962). *A Historical Account of the Development of Forest Management in the Colony.* Government Printer, Nairobi.

Longman K.A. and Jeník, J. (1987). *Tropical Forest and Its Environment*. Second Edition. Longman Group Ltd., London.

Maynard, G.H. and Orcutt, D.M. (1987). *Physiology of Plants Under Stress*. John Wiley & Sons, USA.

Meyer, B.S. and Anderson, B.D. (1952). *Plant Physiology.* D. Van Nostrand Co. Inc., New York.

Meyer, B.S., Anderson, B.D., Bohning, R.H. and Fratianne, D.G. (1975). *Introduction to Plant Physiology*. D. Van Nostrand Co. Inc., New York.

Mihretu, M. (1994). Provenance trials of exotic and indigenous trees. *Research Note No. 3*. Ministry of Natural Resources Development and Environmental Protection, Addis Ababa. 83pp.

Ministry of Environment and Natural Resources (1994). *Kenya Forestry Beyond 2000: An Overview of the Kenya Forestry Master Plan*, Nairobi.

Molyneux, D.E. and Davies, W.J. (1983). Rooting pattern and water relations of three pasture grasses growing in drying soil. *Oecologia* (Berlin) **58**, 220-224.

Mooney, H.A. (1986). Photosynthesis. In: *Plant Ecology* (Ed. M.J. Crawley), pp 345-373.

Morgan, D.C. and Smith, H. (1981). Control of development in *Chenopodium album* L. by shadelight: the effect of light quantity (total fluence rate) and light quality (red:far-red ratio). *New Phytol.* **88,** 239-248.

Murray, D.B. and Nichols, R. (1966). Light, shade and growth in some tropical plants. In: *Light as an Ecological Factor* (Eds. R. Bainbridge, G.C. Evans and O. Rackham), pp 9-263. Blackwell Scientific Publications, Oxford.

Nicholson, D.I. (1960). Light requirements of seedlings of Dipterocapaceae. *Malayan Forester* **23**, 344-356.

Oberbauer, S.F. and Strain, B.R. (1985). Effects of light regime on the growth and physiology of *Pentaclethra macroloba* (Mimosacaea) in Costa Rica. *J. Trop. Ecol.* **1,** 303-320.

Okali, D.U.U. (1971). Rates of dry matter production in some tropical forest tree seedlings. *Annals of Botany* **35**, 87-97.

Okali, D.U.U. (1972). Growth-rates of some West African forest-tree seedlings in shade. *Annals of Botany* **36**, 153-172.

Oldeman R.A.A. and Dijk, J.V. (1991). Diagnosis of the temperament of tropical trees. In: *Rain Forest Regeneration and Management* (Eds. A. Gomez- Pompa, T.C. Whitmore and M. Hadley), pp 21-65.

Osonubi, O. and Davies, W.J. (1981). Root growth and water relations of Oak and Birch seedlings. *Oecologia* (Berlin) **51,** 343-350.

Parry, M.S. (1957). Progress with hardwood replacement in Tanganyika. *Brit. Commonw. For. Conf. Govt.* Printer, Dar-es-Salaam.

Poore, E.E.D. (1968). Studies in Malaysian forests. *J. Ecol.* **56,** 143-196.

Popma, J. and Bongers, F. (1988). The effect of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia* (Berlin) 75, 625-632.

Popma, J. and Bongers, F. (1991). Acclimation of seedlings of three Mexican tropical rain forest tree species to a change in light availability. *J. Trop. Ecol.* **7,** 85-97.

Richards, P.W. (1952). *The Tropical Rain Forest*. Cambridge University Press, London.

Riddoch, I., Lehto, T. and Grace, J. (1991). Photosynthesis of tropical tree seedlings in relation to light and nutrient supply. *New Phytol.* **119**, 137-147.

Sahni, K.C. (1968). *Important Trees of the Northern Sudan.* Khartoum University Press, Khartoum.

Salisbury, F.B. and Ross, C.W. (1978). *Plant Physiology*. Wadsworth, California. 2nd Ed.

Sasaki, S. and Mori, T. (1981). Growth responses of dipterocarp seedlings to light. *Malaysian Forester* **44**, 319-345.

Sharew, H. (1994). Regeneration of *Juniperus procera* and *Afrocarpus gracilior* in the afromontane forests of Ethiopia. PhD thesis, University of Edinburgh.

Sinclair, T.R., Goudriaan, J. and De Wit, C.T. (1977). Mesophyll resistance and CO_2 compensation concentration in leaf photosynthesis models. *Photosynthetica* **11,** 56-65.

Smith, H. (1981a). Adaptation to shade. In: *Physiological Processes Limiting Plant Growth* (Ed. C.B. Johnson), pp 159 -172. Butterworths, London.

Smith, H. (1981b). Light quality as an ecological factor. In: *Plants and their Atmospheric Environment* (Eds. J. Grace, E.D. Ford and P.G. Jarvis), pp 93-110. Blackwell Scientific Publications, Oxford.

Smith, H. (1982). Light quality, photoperception, and plant strategy. *Ann. Rev. Plant Physio.* **33,** 481-518.

Specht, R.L. and Grove, R.H. (1966). Comparison of phosphorus nutrition of Australian heath plants and introduced economic plants. *Aust. J. Bot.* **14**, 201 - 221.

Stoutjesdijk, P.H. (1972). A note on the spectral transmission of light by tropical rainforest. *Acta Bot. Neerl.* **21,** 346-350.

Street, H.E. and Öpik, H. (1984). *The Physiology of Flowering Plants: The Growth and Development.* Edward Arnold, London.

Synnott, T.J. (1975). Factors affecting the regeneration and growth of *Entadrophragma utile* (Dawe and Sprague). PhD thesis, University of Oxford.

Teel, W. (1984). *A Pocket Dictionary of Trees and Seeds in Kenya.* KENGO, Nairobi.

Thompson, W.A., Stocker, G.C. and Kriedemann, P.E. (1988). Growth and photosynthetic response to light and nutrients of *Flindersia brayleyana* F. Muell, a rain forest tree with broad tolerance to sun and shade. *Aust. J. Plant. Physio.* **15,** 299-315.

Trapnell, C.G. and Langdale-Brown, I. (1962). The natural vegetation of East Africa. In: *The Natural Resources of East Africa* (Ed. E.W. Russell), pp 92-102. D.A. Hawkins Ltd and E. Afr. Literature Bureau, Nairobi.

Turner, I.M. and Newton, A.C. (1990). The initial responses of some tropical rain forest seedlings to a large gap environment. *J. App. Ecol.* **27,** 605-608.

Warrington, I.J., Rook, D.A., Morgan, D.C. and Turnbull, H.L. (1988). The influence of simulated shadelight and daylight on growth, development and photosynthesis of *Pinus radiata, Agathis australis* and *Dacrydium cupressinum. Plant Cell and Environment* **11,** 343-386.

White, F. (1962). *Forest Flora of Northern Rhodesia.* Oxford University Press, Oxford.

Whitmore, T.C. (1985). *Tropical Rain Forests of the Far East*. Clarendon Press, Oxford.

Whitmore, T.C. (1989). Canopy gaps and two major groups of forest trees. *Ecol*. **70,** 536-538.

Whitmore, T.C. and Bowen, M.R. (1983). Growth analyses of some *Agathis* species. *Malaysian Forester* **46,** 186-196.

APPENDIX I
ANOVA TABLES FOR RESULTS IN CHAPTER 3

Appendix I A: Analysis of variance table for total plant dry weight in the final harvest

Source of variation	df	ss	ms	F-value	Level of significance
Main plots:					
Blocks	2	0.5125	0.2562	2.98	ns
Light	3	6.2813	2.0939	24.31	***
Error	6	0.5167	0.0861		
Sub-plots:					
Species	1	20.6667	20.666	176.71	****
Light x Species	3	2.3998	7	6.84	*
Error	8	0.9356	0.7999		
			0.1169		
Sub-subplots:					
Nutrient	1	9.0915	9.0915	136.49	****
Light x Nutrient	3	0.8638	0.2879	4.32	*
Species x Nutrient	1	3.2158	3.2158	48.28	***
Light x Species x Nutrient	3	0.6033	0.2011	3.02	*
Error	16	1.0658	0.0666		
Total	47	46.1527			

Symbols:

ns = not significant at $P<0.05$;
* = significant at $P<0.05$;
** = significant at $P<0.0l$;
*** = significant at $P<0.001$; and
**** = significant at $P<0.0001$.

Appendix I B: Analysis of variance table for mean height in the final harvest

Source of variation	df	ss	ms	F-value	Level of significance
Main plots:					
Blocks	2	6.5478	3.2739	15.47	**
Light	3	16.5946	5.5315	26.15	***
Error	6	1.2693	0.2116		
Sub-plots:					
Species	1	6.1920	6.1920	8.06	*
Light x Species	3	7.0882	2.3627	3.08	ns
Error	8	6.1465	0.7683		
Sub-subplots:					
Nutrient	1	45.5910	45.5910	160.81	***
Light x Nutrient	3	0.6082	0.2027	0.72	ns
Species x Nutrient	1	3.8082	3.3082	11.67	**
Light x Species x Nutrient	3	4.3121	1.4374	5.07	*
Error	16	4.5365	0.2835		
Total	47	102.6944			

Appendix I C: Analysis of variance for number of leaves in the final harvest

Source of variation	df	ss	ms	F-value	Level of significance
Main plots:					
Blocks	2	2.3712	0.1856	6.94	*
Light	3	54.5567	18.1856	106.47	****
Error	6	1.0246	0.1708		
Sub-plots:					
Species	1	32.3408	32.3408	26.46	****
Light x Species	3	2.8617	0.9539	0.78	ns
Error	8	9.7775	1.2222		
Sub-subplots:					
Nutrient	1	7.5208	7.5208	8.17	*
Light x Nutrient	3	4.3950	1.4650	1.59	ns
Species x Nutrient	1	0.0009	0.0009	< 1	ns
Light x Species x Nutrient	3	1.9399	0.6466	< 0.70	ns
Error	16	14.7234	0.9202		
Total	47	131.5125			

Appendix I D: Analysis of variance table for number of leaves shed by the final harvest

Source of variation	df	ss	ms	F-value	Level of significance
Main plots:					
Blocks	2	0.3617	0.1808	0.97	ns
Light	3	6.0966	2.0322	10.94	**
Error	6	1.1140	0.1857		
Sub-plots:					
Species	1	57.8602	57.8602	271.07	****
Light x Species	3	5.9097	1.9699	9.23	**
Error	8	1.7076	0.2134		
Sub-subplots:					
Nutrient	1	5.5352	5.5352	59.97	***
Light x Nutrient	3	4.7547	1.5849	17.17	**
Species x Nutrient	1	5.4002	5.4002	58.51	****
Light x Species x Nutrient	3	3.6382	1.2127	13.14	***
Error	16	1.4767	0.0923		
Total	47	93.8548			

Appendix I E: Analysis of variance table for leaf area per seedling in the final harvest

Source of variation	df	ss	ms	F-value	Level of significance
Main plots:					
Blocks	2	7634.35	3817.18	6.93	*
Light	3	26102.19	8700.73	15.79	**
Error	6	3305.70	550.95		
Sub-plots:					
Species	1	359303.73	359303.73	677.88	****
Light x Species	3	16949.59	5649.86	10.68	**
Error	8	8240.33	530.04		
Sub-subplots:					
Nutrient	1	137569.97	137569.97	141.63	****
Light x Nutrient	3	5227.02	1742.34	1.79	ns
Species x Nutrient	1	39222.04	39222.04	40.38	****
Light x Species x Nutrient	3	5212.42	1737.47	1.79	ns
Error	16	15541.20	971.33		
Total	47	624308.63			

Appendix I F: Analysis of variance table for relative growth rate (RGR)

Source of variation	df	ss	ms	F-value	Level of significance
Main plots:					
Blocks	2	0.009630	0.004615	3.76	ns
Light	3	0.035842	0.011947	9.74	*
Error	6	0.007363	0.001227		
Sub-plots:					
Species	1	0.092752	0.092752	41.63	***
Light x Species	3	0.000611	0.000203	0.09	ns
Error	8	0.017825	0.002228		
Sub-subplots:					
Nutrient	1	0.022533	0.022533	22.29	***
Light x Nutrient	3	0.011441	0.003814	3.77	*
Species x Nutrient	1	0.019360	0.019360	19.15	***
Light x Species x Nutrient	3	0.025220	0.008407	8.32	**
Error	16	0.016172	0.001011		
Total	47	0.258749			

Appendix I G: Analysis of variance table for net assimilation rate (NAR)

Source of variation	df	ss	ms	F-value	Level of significance
Main plots:					
Blocks	2	92.6075	46.3038	2.94	ns
Light	3	2292.9457	764.3152	48.53	***
Error	6	94.4883	15.7480		
Sub-plots:					
Species	1	354.0360	354.0360	14.97	***
Light x Species	3	15.7618	5.2539	0.22	ns
Error	8	189.1922	23.6490		
Sub-subplots:					
Nutrient	1	12.3019	12.3019	1.05	ns
Light x Nutrient	3	98.8581	32.9527	2.80	ns
Species x Nutrient	1	79.1560	79.1560	6.73	*
Light x Species x Nutrient	3	294.5419	98.1806	8.34	**
Error	16	188.2434	11.7652		
Total	47	3712.1328			

Appendix I H: Analysis of variance table for leaf area ratio (LAR) in the final harvest

Source of variation	df	ss	ms	F-value	Level of significance
Main plots:					
Blocks	2	93.2803	49.1402	0.37	ns
Light	3	29162.438	9720.8127	73.16	****
Error	6	0	132.8789		
		797.2733			
Sub-plots:					
Species	1	2783.8917	2783.8917	18.97	**
Light x Species	3	1374.5223	458.1741	3.1218	ns
Error	8	1174.0637	146.7680		
Sub-subplots:					
Nutrient	1	93.2698	93.2698	4.00	ns
Light x Nutrient	3	463.9257	154.6419	6.63	**
Species x Nutrient	1	2371.7814	2371.7814	101.66	****
Light x Species x Nutrient	3	395.1234	131.7078	5.65	*
Error	16	373.2724	23.3295		
Total	47	39087.842			
		9			

Appendix I J: Analysis of variance table for specific leaf area (SLA) in the final harvest

Source of variation	df	ss	ms	F-value	Level of significance
Main plots:					
Blocks	2	586.5139	293.2570	1.34	ns
Light	3	71243.858	23747.953	108.96	****
Error	6	9	0		
		1307.6794	217.9466		
Sub-plots:					
Species	1	769.7610	769.7610	3.16	ns
Light x Species	3	3216.0762	1072.0254	4.40	**
Error	8	1946.8955	243.3619		
Sub-subplots:					
Nutrient	1	2234.5052	2234.5052	21.43	***
Light x Nutrient	3	1288.0567	429.3522	4.12	*
Species x Nutrient	1	4356.3541	4356.3541	41.78	****
Light x Species x Nutrient	3	1025.1289	341.7096	3.28	*
Error	16	1668.1101	104.2569		
Total	47	89624.939			
		7			

Appendix I K: Analysis of variance table for leaf weight ratio (LWR) in the final harvest

Source of variation	df	ss	ms	F-value	Level of significance
Main plots:					
Blocks	2	0.005879	0.0094	1.90	ns
Light	3	0.004021	0.001340	0.87	ns
Error	6	0.009259	0.001543		
Sub-plots:					
Species	1	0.02960	0.029601	76.76	****
Light x Species	3	0.002655	0.000885	2.29	ns
Error	8	0.003085	0.000385		
Sub-subplots:					
Nutrient	1	0.03030	0.03030	56.78	****
Light x Nutrient	3	0.000173	0.000058	0.11	ns
Species x Nutrient	1	0.001900	0.001900	3.56	ns
Light x Species x Nutrient	3	0.000548	0.000183	0.35	ns
Error	16	0.009539	0.000534		
Total	47	0.095961			

Appendix I L: Analysis of variance table for stem weight ratio (SWR) in the final harvest

Source of variation	df	ss	ms	F-value	Level of significance
Main plots:					
Blocks	2	0.0009599	0.0004300	12.46	**
Light	3	0.0004337	0.0001447	4.19	ns
Error	6	0.0002070	0.0000345		
Sub-plots:					
Species	1	0.005590	0.0055901	144.87	****
Light x Species	3	0.000391	0.0001303	3.38	
Error	8	0.000154	0.0000193		
Sub-subplots:					
Nutrient	1	0.0000021	0.0000021	0.004	ns
Light x Nutrient	3	0.0001809	0.000060	0.01	ns
Species x Nutrient	1	0.000507	0.000507	0.08	ns
Light x Species x Nutrient	3	0.000191	0.000073	0.01	ns
Error	16	0.095514	0.005969		
Total	47	0.104040			

Appendix I M: Analysis of variance table for root weight ratio (RWR) in the final harvest

Source of variation	df	ss	ms	F-value	Level of significance
Main plots:					
Blocks	2	0.00937	0.004688	3.36	
Light	3	0.00658	0.002194	1.57	ns
Error	6	0.008369	0.001394		
Sub-plots:					
Species	1	0.00918	0.009185	28.59	****
Light x Species	3	0.00256	0.000854	2.66	ns
Error	8	0.00256	0.001321		
Sub-subplots:					
Nutrient	1	0.02940	0.029403	73.12	****
Light x Nutrient	3	0.00041	0.000139	0.35	ns
Species x Nutrient	1	0.00036	0.000363	0.90	ns
Light x Species x Nutrient	3	0.00147	0.000491	1.22	ns
Error	16	0.00643	0.000402		
Total	47	0.076736			

Appendix I N: Analysis of variance table for shoot root ratio (SRR) in the final harvest

Source of variation	df	ss	ms	F-value	Level of significance
Main plots:					
Blocks	2	2.8930	1.4464	2.93	ns
Light	3	1.9339	0.6446	1.31	ns
Error	6	2.9638	0.4940		
Sub-plots:					
Species	1	2.8130	2.8130	29.15	***
Light x Species	3	1.5970833	0.3530	3.66	ns
Error	8	0.7719	0.0964		
Sub-subplots:					
Nutrient	1	8.8234	8.8234	77.96	****
Light x Nutrient	3	0.3788	0.1262	1.12	ns
Species x Nutrient	1	0.0040	0.0004	0.04	ns
Light x Species x Nutrient	3	0.5710	0.1903	1.68	ns
Error	16	1.8109	0.1132		
Total	47	24.0231			

APPENDIX II
SUMMARY OF MEAN VALUES IN CHAPTER 4

Appendix II A: Summary of mean total dry weight in the final harvest, g

Previous light, % full sunlight	Present light, % full sunlight	*C. africana*, low nutrient	*C. africana*, high nutrient	*V. keniensis*, low nutrient	*V. keniensis*, high nutrient
19	13	2.42	7.52	1.03	1.62
	35	3.70	5.80	1.12	3.42
	47	4.46	11.28	1.17	4.53
	100	5.46	11.34	1.17	4.53
44	13	6.23	16.27	0.59	4.67
	35	6.36	17.78	2.06	5.14
	47	5.53	23.62	2.55	4.06
	100	7.00	20.43	2.22	4.28
52	13	6.15	14.03	1.88	4.75
	35	4.52	21.22	2.24	4.74
	47	5.53	22.07	3.01	2.77
	100	7.72	20.71	2.59	3.63
100	13	9.08	12.44	1.51	4.09
	35	8.22	23.16	2.29	4.70
	47	8.27	25.06	3.08	8.06
	100	11.29	29.46	3.36	7.20

Appendix II B: Summary of mean relative growth rate (RGR), g g^{-1} wk^{-1}

Previous light, % full sunlight	Present light, % full sunlight	*C. africana*, low nutrient	*C. africana*, high nutrient	*V. keniensis*, low nutrient	*V. keniensis*, high nutrient
19	13	-0.053	0.037	0.055	0.078
	35	0.144	0.058	0.080	0.197
	47	0.167	0.236	0.272	0.393
	100	0.196	0.191	0.273	0.056
44	13	0.118	0.160	0.109	0.200
	35	0.164	0.149	0.164	0.251
	47	0.050	0.267	0.112	0.112
	100	0.090	0.21	0.115	0.257
52	13	0.131	0.137	0.165	0.123
	35	0.104	0.234	0.257	0.256
	47	0.068	1.194	0.331	0.050
	100	0.167	0.266	0.223	0.085
100	13	0.131	-0.021	0.016	0.037
	35	0.172	0.142	-0.023	0.136
	47	0.036	0.129	0.140	0.382
	100	0.138	0.210	0.275	0.252

Appendix II C: Mean net assimilation rates (NAR), g m^{-2} wk^{-1}

Previous light, % full sunlight	Present light, % full sunlight	*C. africana*, low nutrient	*C. africana*, high nutrient	*V. keniensis*, low nutrient	*V. keniensis*, high nutrient
19	13	8.27	14.35	6.01	4.69
	35	16.07	8.40	8.20	16.47
	47	16.94	20.90	20.79	23.17
	100	20.65	23.31	23.25	7.93
44	13	15.75	13.47	10.69	19.51
	34	21.73	19.07	17.43	26.34
	47	12.14	34.99	15.04	25.88
	100	11.11	29.36	15.17	21.77
52	13	17.02	13.66	18.55	8.40
	35	9.39	26.18	28.86	15.28
	47	12.12	23.51	43.84	3.28
	100	24.17	36.15	15.95	10.08
100	13	21.44	-0.20	2.60	0.80
	35	31.46	22.06	0.93	13.25
	47	5.74	20.17	12.20	41.93
	100	28.17	36.78	40.34	31.49

Appendix II D: Mean leaf area ratio (LAR) in the final harvest, cm^2 g^{-1}

Previous light, % full sunlight	Present light, % full sunlight	*C. africana*, low nutrient	*C. africana*, high nutrient	*V. keniensis*, low nutrient	*V. keniensis*, high nutrient
19	13	102.9	124.4	115.6	128.7
	35	106.4	114.3	101.1	98.8
	47	81.6	91.3	83.9	75.3
	100	81.6	77.4	77.8	98.5
44	13	73.4	104.2	107.9	117.3
	35	66.0	88.1	67.7	90.7
	47	69.5	75.6	71.2	90.8
	100	66.14	59.3	74.9	75.2
52	13	70.4	100.8	121.5	123.3
	35	70.5	82.7	81.0	97.4
	47	68.9	73.1	69.2	110.9
	100	70.7	61.7	67.5	70.8
100	13	63.3	103.4	119.7	112.3
	35	45.9	62.3	73.9	88.7
	47	52.8	63.2	66.2	83.5
	100	43.5	50.1	53.8	69.1

Appendix II E: Summary of mean specific leaf are (SLA) in the final harvest, $cm^2\ g^{-1}$

Previous light, % full sunlight	Present light, % full sunlight	*C. africana,* low nutrient	*C. africana,* high nutrient	*V. keniensis,* low nutrient	*V. keniensis* high nutrient
19	13	224.1	259.8	225.3	248.5
	35	170.1	216.8	200.1	174.0
	47	178.0	193.9	169.5	146.2
	100	195.1	151.9	164.1	176.4
44	13	171.5	198.1	231.9	201.4
	35	162.1	176.2	192.7	160.9
	47	159.0	175.1	153.3	178.1
	100	151.0	122.5	152.5	167.6
52	13	170.9	197.0	250.8	203.4
	35	159.8	161.1	176.3	179.8
	47	152.1	161.7	147.8	209.6
	100	165.1	145.2	139.3	133.2
100	13	175.6	194.0	250.2	173.0
	35	130.2	145.0	167.4	161.3
	47	131.7	134.0	149.9	165.1
	100	118.6	120.2	118.7	130.9

Appendix II F: Summary of mean leaf weight ratio (LWR) in the final harvest

Previous light, % full sunlight	Present light, % full sunlight	*C. africana,* low nutrient	*C. africana,* high nutrient	*V. keniensis,* low nutrient	*V. keniensis,* high nutrient
19	13	0.45	0.53	0.50	0.55
	35	0.46	0.54	0.50	0.57
	47	0.47	0.48	0.50	0.52
	100	0.41	0.50	0.47	0.55
44	13	0.42	0.44	0.46	0.58
	35	0.40	0.50	0.44	0.57
	47	0.43	0.47	0.46	0.50
	100	0.44	0.49	0.44	0.55
52	13	0.41	0.52	0.47	0.55
	35	0.44	0.51	0.43	0.55
	47	0.45	0.45	0.48	0.55
	100	0.14	0.49	0.46	0.54
100	13	0.38	0.54	0.44	0.56
	35	0.35	0.44	0.44	0.55
	47	0.44	0.47	0.43	0.50
	100	0.36	0.42	0.43	0.54

Appendix II G: Summary of mean stem weight ratio (SWR) in the final harvest

Previous light, % full sunlight	Present light, % full sunlight	*C. africana*, low nutrient	*C. africana*, high nutrient	*V. keniensis*, low nutrient	*V. keniensis*, high nutrient
19	13	0.25	0.28	0.29	0.27
	35	0.24	0.25	0.24	0.24
	47	0.24	0.27	0.24	0.28
	100	0.26	0.21	0.20	0.23
44	13	0.24	0.36	0.25	0.26
	35	0.23	0.29	0.28	0.24
	47	0.22	0.28	0.24	0.30
	100	0.23	0.23	0.20	0.23
52	13	0.25	0.30	0.22	0.27
	35	0.22	0.26	0.23	0.28
	47	0.22	0.27	0.23	0.25
	100	0.22	0.24	0.20	0.24
100	13	0.20	0.24	0.24	0.26
	35	0.20	0.25	0.27	0.24
	47	0.20	0.26	0.26	0.24
	100	0.19	0.26	0.17	0.20

Appendix II H: Summary of mean root weight ratio (RWR) in the final harvest

Previous light, % full sunlight	Present light, % full sunlight	*C. africana*, low nutrient	*C. africana*, high nutrient	*V. keniensis*, low nutrient	*V. keniensis*, high nutrient
19	13	0.30	0.19	0.21	0.19
	35	0.30	0.21	0.26	0.19
	47	0.29	0.25	0.27	0.20
	100	0.33	0.29	0.32	0.22
44	13	0.34	0.20	0.29	0.16
	35	0.37	0.21	0.27	0.19
	47	0.35	0.26	0.30	0.20
	100	0.34	0.28	0.30	0.22
52	13	0.34	0.18	0.32	0.18
	35	0.34	0.22	0.34	0.16
	47	0.33	0.27	0.30	0.20
	100	0.38	0.26	0.34	0.22
100	13	0.43	0.21	0.31	0.18
	35	0.45	0.31	0.28	0.21
	47	0.41	0.27	0.31	0.26
	100	0.45	0.32	0.40	0.27

Appendix II J : Summary of mean shoot root ratio (SRR) in the final harvest

Previous light, % full sunlight	Present light, % full sunlight	*C. africana,* low nutrient	*C. africana* high nutrient	*V. keniensis* low nutrient	*V. keniensis* high nutrient
19	13	2.4	4.3	3.7	4.4
	35	2.3	3.2	2.9	4.2
	47	2.5	2.9	2.8	4.2
	100	2.0	2.5	2.1	3.6
44	13	1.9	4.1	2.5	5.2
	35	1.7	3.8	2.6	4.4
	47	1.9	2.9	2.3	5.0
	100	2.0	2.6	2.4	4.3
52	13	1.9	4.5	2.2	4.6
	35	1.9	3.5	1.9	5.1
	47	2.4	2.7	2.4	4.1
	100	1.6	2.8	1.9	3.6
100	13	1.3	3.8	2.2	4.4
	35	1.2	2.2	2.5	3.7
	47	1.4	2.7	2.2	2.8
	100	1.2	2.1	1.5	2.6

Appendix II K: Summary on mean height in the final measurement, cm

Previous light, % full sunlight	Present light, % full sunlight	*C. africana,* low nutrient	*C. africana,* high nutrient	*V. keniensis,* low nutrient	*V. keniensis,* high nutrient
19	13	11.4	22.1	11.3	13.0
	35	12.1	16.3	10.7	14.2
	47	11.7	21.7	11.0	16.7
	100	11.9	16.7	12.1	12.1
44	13	12.9	28.3	14.3	16.8
	35	13.3	31.7	13.5	17.0
	47	11.7	30.5	12.0	14.9
	100	12.6	22.1	11.9	14.6
52	13	13.5	29.3	12.2	16.2
	35	10.9	28.0	10.1	17.0
	47	11.3	28.8	12.9	12.0
	100	12.8	24.4	12.6	13.4
100	13	13.4	26.9	10.7	16.6
	35	11.0	28.0	11.9	14.9
	47	12.3	28.9	13.3	16.1
	100	12.4	26.1	11.4	14.4

Appendix II L: Summary of mean leaf area per seedling in the final harvest, cm^2

Previous light, % full sunlight	Present light, % full sunlight	*C. africana.* low nutrient	*C. africana,* high nutrient	*V. keniensis,* low nutrient	*V. keniensis,* high nutrient
19	13	241.3	887.0	118.3	217.9
	35	281.4	604.3	111.3	335.3
	47	267.6	997.0	147.0	304.7
	100	426.1	857.4	156.9	200.3
44	13	399.5	1428.0	214.3	533.1
	35	407.9	1534.3	169.4	464.4
	47	368.5	1697.3	175.9	380.2
	100	468.4	1204.2	143.0	318.0
52	13	428.1	1436.4	197.5	532.1
	35	300.1	1747.7	170.1	463.7
	47	364.0	1586.6	203.8	319.7
	100	508.4	1268.6	163.4	255.4
100	13	540.8	1254.6	160.0	477.6
	35	375.2	1497.2	119.6	423.5
	47	425.2	1612.2	191.0	654.3
	100	482.7	1465.5	174.8	489.0

Appendix II M: Summary of mean number of leaves present in the final harvest

Previous light, % full sunlight	Present light, % full sunlight	*C. africana,* low nutrient	*C. africana,* high nutrient	*V. keniensis,* low nutrient	*V. keniensis,* high nutrient
19	13	8.6	10.0	12.4	16.0
	35	9.4	7.4	11.2	12.8
	47	8.6	10.2	13.8	11.8
	100	11.8	10.6	18.2	13.4
44	13	11.2	10.0	12.4	18.2
	35	10.6	11.6	13.0	12.0
	47	10.6	11.2	13.8	12.6
	100	10.2	11.4	13.8	14.0
52	13	11.6	9.8	13.0	12.8
	35	10.6	11.0	15.0	16.0
	47	8.6	11.6	15.4	19.6
	100	10.6	13.0	14.2	12.2
100	13	10.6	9.2	14.2	15.6
	35	11.6	9.8	14.4	13.0
	47	10.8	11.8	15.8	27.8
	100	11.4	13.2	18.4	16.0

Appendix II N: Summary of the number of leaves shed between the first and final harvest

Previous light, % full sunlight	Present light, % full sunlight	*C. africana,* low nutrient	*C. africana,* high nutrient	*V. keniensis,* *low nutrient*	*V. keniensis,* high nutrient
19	13	1.8	2.2	0.8	1.0
	35	0.0	3.8	0.0	1.0
	47	0.2	1.4	0.4	1.6
	100	0.6	2.2	0.0	1.4
44	13	0.8	2.0	0.6	2.0
	35	0.2	2.4	1.2	1.4
	47	1.4	2.6	1.0	2.6
	100	1.2	1.8	0.6	2.4
52	13	1.0	3.6	1.0	2.6
	35	1.6	1.8	0.6	2.0
	47	1.0	1.0	0.2	1.4
	100	0.4	3.8	1.0	1.2
100	13	3.0	4.4	1.6	5.4
	35	1.0	2.0	1.0	4.8
	47	2.6	2.4	1.8	6.0
	100	1.2	1.6	1.0	1.0

APPENDIX III
ANOVA TABLES FOR RESULTS IN CHAPTER 4

Appendix III A: Analysis of variance table for total dry weight in the final harvest

Source of variation	Sum of Squares ss	Degrees of Freedom df	Mean Square ms	F	Level of significance
Present light, T	91.2076	3	30.4024	9.03	**
Previous light, P	269.8394	3	89.9465	27.71	****
Species, S	1214.9582	1	1214.9582	360.84	****
Nutrient, N	714.5440	1	747.5440	222.02	****
T x P	28.5169	9	3.1685	0.94	ns
T x S	39.4988	3	13.1663	3.91	ns
T x N	26.8535	3	8.9512	2.66	ns
P x S	117.0564	3	39.0188	11.59	**
P x N	71.6070	3	23.8690	7.09	**
S x N	331.7406	1	331.7406	98.53	****
T x P x S	14.7871	9	1.6430	0.49	ns
T x P x N	32.6265	9	3.6252	1.08	ns
T x S x N	34.1135	3	11.3712	3.38	ns
P x S x N	43.8071	3	14.6024	434	*
Error	30.3026	9	3.3670		
Total	3094.4593	63			

Appendix III B: Analysis of variance table for relative growth rate (RGR)

Source	Sum of squares ss	Degrees of freedom df	Mean square ms	F	Level of significance
Present light, T	0.10294	3	0.034031	6.79	*
Previous light, P	0.007264	3	0.002421	0.48	ns
Species, S	0.010100	1	0.010100	2.02	ns
Nutrient, N	0.012100	1	0.012100	2.42	ns
T x P	0.099521	9	0.011058	2.21	ns
T x S	0.017488	3	0.005829	1.16	ns
T x N	0.007256	3	0.002419	0.48	ns
P x S	0.011521	3	0.003840	0.77	ns
P x N	0.033548	3	0.011183	2.23	ns
S x N	0.007526	2	0.007526	1.50	ns
T x P x S	0.054852	9	0.006095	1.22	ns
T x P x N	0.048702	9	0.005411	1.08	ns
T x S x N	0.023630	3	0.007877	1.57	ns
P x S x N	0.068952	3	0.022984	4.59	*
Error	0.045077	9	0.005008		
Total	0.549631	63			

Appendix III C: Analysis of variance table for net assimilation rate (NAR)

Source	Sum of Squares ss	Degrees of Freedom df	Mean Square ms	F	Level of Significance
Present light, T	1405.1915	3	468.3972	9.20	**
Previous light, P	224.3145	3	74.7715	1.47	ns
Species, S	65.0644	1	65.0644	1.28	ns
Nutrient, N	56.6444	1	56.64444	1.11	ns
T x P	830.6420	9	92.29	1.81	ns
T x S	265.0795	3	88.3598	1.74	ns
T x N	9.0923	3	3.0309	0.60	ns
P x S	202.9109	3	67.6370	1.33	ns
P x N	362.8190	3	120.9397	2.38	ns
S x N	97.9852	1	97.9852	1.92	ns
T x P x S	788.8182	9	87.1816	1.72	ns
T x P x N	784.6343	9	87.6465	1.71	ns
T x S x N	361.4880	3	120.4960	2.37	ns
P x S x N	721.1764	3	240.39	4.72	*
Error	458.1155	9	50.9017		
Total	6633.9761				

Appendix III D: Analysis of variance table for leaf area ratio (LAR) in the final harvest

Source	Sum of Squares ss	Degrees of Freedom df	Mean Square ms	F	Level of Significance
Present light, T	12621.2680	3	4233.7560	20.56	***
Previous light, P	5345.9781	3	1782.3260	8.67	**
Species, S	4054.5056	1	4054.5056	19.73	**
Nutrient, N	1117.2306	1	1117.2306	5.44	*
T x P	1659.6681	9	184.4076	0.90	ns
T x S	834.3681	3	278.1227	1.35	ns
T x N	1481.3456	3	493.78	2.40	ns
P x S	668.6681	3	222.8894	1.08	ns
P x N	424.0331	3	141.3444	0.69	ns
S x N	261.5306	1	261.6306	1.27	ns
T x P x S	1471.5356	9	163.5040	0.80	ns
T x P x N	1127.5731	9	125.2859	0.61	ns
T x S x N	1386.8231	3	462.2744	2.50	ns
P x S x N	461.4106	3	153.8035	0.75	ns
Error	1849.1006	9	205.4556		
Total	34816.1394	63			

Appendix III E: Analysis of variance table for specific leaf area in the final harvest

Source	Sum of Squares ss	Degrees of Freedom df	Mean Square ms	F	Level of Significance
Present light, T	35466.7310	3	11822.2440	27.41	****
Previous light, P	14251.8750	3	4750.6250	11.01	**
Species, S	1312.2506	1	1312.2505	3.04	ns
Nutrient, N	153.7600	1	153.7600	0.36	ns
T x P	2075.8181	9	230.6465	0.53	ns
T x S	1258.8556	3	419.5185	0.97	ns
T x N	3473.8556	3	1157.8935	2.68	ns
P x S	1219.1512	3	406.3838	0.94	ns
P x N	369.4212	3	123.1404	0.29	ns
S x N	1089.0000	1	1089.0000	2.52	ns
T x P x S	2324.4231	9	258.2692	0.60	ns
T x P x N	3456.5975	9	385.0664	0.89	ns
T x S x N	5548.4162	4	1849.4721	4.29	*
P x S x N	413.6112	4	137.8704	0.32	ns
Error	3881.9125	9	431.3236		
Total	76304.5044				

Appendix III F: Analysis of variance table for leaf weight ratio (LWR) in the final harvest

Source	Sum of Squares ss	Degrees of Freedom df	Mean Square ms	F	Level of Significance
Present light, T	0.001288	3	0.000429	1.39	ns
Previous light, P	0.021912	3	0.007304	23.69	****
Species, S	0.051756	1	0.051756	167.86	****
Nutrient, N	0.113906	1	0.113906	369.43	****
T x P	0.015050	9	0.001672	5.42	**
T x S	0.003406	3	0.001135	3.68	ns
T x N	0.003881	3	0.001294	4.20	*
P x S	0.013556	3	0.004519	14.66	***
P x N	0.004781	3	0.001594	5.17	*
S x N	0.000025	1	0.000025	0.08	ns
T x P x S	0.022706	9	0.002523	8.18	**
T x P x N	0.005306	9	0.000590	1.91	ns
T x S x N	0.004412	3	0.001471	4.77	*
P x S x N	0.000738	3	0.000246	0.80	ns
Error	0.002775	9	0.000308		
Total	0.265498	63			

Appendix III G: Analysis of variance table for stem weight ratio (SWR) in the final harvest

Source	Sum of Squares ss	Degrees of Freedom df	Mean Square ms	F	Level of Significance
Present light, T	0.012367	3	0.004122	10.45	**
Previous light, P	0.006942	3	0.002314	5.86	*
Species, S	0.000002	1	0.000002	0.00	ns
Nutrient, N	0.011290	1	0.011290	28.61	***
T x P	0.001752	9	0.000195	0.49	ns
T x S	0.001780	3	0.000593	1.50	ns
T x N	0.000655	3	0.000218	0.55	ns
P x S	0.001942	3	0.000647	1.64	ns
P x N	0.002042	3	0.000681	1.73	ns
S x N	0.002889	1	0.002889	7.32	*
T x P x S	0.005939	9	0.0006599	1.67	ns
T x P x N	0.004802	9	0.0005335	1.35	ns
T x S x N	0.001842	3	0.000614	1.56	ns
P x S x N	0.003792	3	0.001264	3.20	ns
Error	0.003552	9	0.000395		
Total	0.061588	63			

Appendix III H: Analysis of variance table for root weight ratio (RWR) in the final harvest

Source	Sum of Squares ss	Degrees of Freedom df	Mean Square ms	F	Level of Significance
Present light, T	0.029305	3	0.009768	16.20	***
Previous light, P	0.043342	3	0.014447	23.96	****
Species, S	0.035627	1	0.035627	59.09	****
Nutrient, N	0.169127	1	0.169127	280.5	****
T x P	0.004889	9	0.000543	0.90	ns
T x S	0.000142	3	0.000047	0.08	ns
T x N	0.006930	3	0.002310	3.83	ns
P x S	0.005217	3	0.001739	2.88	ns
P x N	0.013330	3	0.004443	7.37	**
S x N	0.000352	1	0.000352	0.58	ns
T x P x S	0.008177	9	0.000908	1.51	ns
T x P x N	0.005302	9	0.000589	0.98	ns
T x S x N	0.002817	3	0.000939	1.56	ns
P x S x N	0.004520	3	0.001527	2.53	ns
Error	0.005427	9	0.000603		
Total	0.334504	63			

Appendix III J: **Analysis of variance table for shoot/root ratio (SRR) in the final harvest.**

Source	Sum of Squares ss	Degrees of Freedom df	Mean Square ms	F	Level of Significance
Present light, T	6.8438	3	2.2812	17.28	***
Previous light, P	6.3438	3	2.1146	16.02	***
Species, S	8.8506	1	8.8506	67.04	****
Nutrient, N	37.2100	1	37.2100	281.86	****
T x P	0.5100	9	0.05667	0.43	ns
T x S	0.2306	3	0.07688	0.58	ns
T x N	0.3506	3	0.1169	0.89	ns
P x S	2.5112	3	0.8371	6.34	*
P x N	1.8962	3	0.6321	4.79	*
S x N	0.7656	1	0.7656	5.8	*
T x P x S	0.6681	9	0.0742	0.56	ns
T x P x N	1.2925	9	0.1436	1.09	ns
T x S x N	0.7756	3	0.2585	1.96	ns
P x S x N	0.7006	3	0.2335	1.77	ns
Error	1.1881	9	0.1320		
Total	70.1375	63			

Appendix III K: **Analysis of variance table for shoot/root ratio (SRR) in the final harvest**

Source	Sum of Squares ss	Degrees of Freedom df	Mean Square ms	F	Level of Significance
Present light, T	30.1555	3	10.0518	3.72	ns
Previous light, P	104.43424	3	34.8114	12.9	**
Species, S	479.0626	1	479.0626	177.48	****
Nutrient, N	1060.3164	1	1060.3164	392.83	****
T x P	23.8089	9	2.6454	0.98	ns
T x S	6.3692	3	2.1231	0.79	ns
T x N	38.4280	3	12.8093	4.75	*
P x S	30.6630	3	10.2290	3.79	ns
P x N	51.2592	3	17.0864	6.33	*
S x N	423.8452	1	423.8452	157.03	****
T x P x S	12.9077	9	1.4342	0.53	ns
T x P x N	24.2489	9	2.6943	1.00	ns
T x S x N	9.5367	3	3.1789	1.18	ns
P x S x N	41.9330	3	13.9777	5.18	*
Error	24.3927	9	2.6992		
Total	2361.2611	63			

Appendix III L: Analysis of variance table for leaf area per seedling in the final harvest

Source	Sum of Squares ss	Degrees of Freedom df	Mean Square ms	F	Level of Significance
Present light, T	39465.84	3	13155.28	3.72	ns
Previous light, P	727424.75	3	242474.92	24.08	ns
Species, S	5293162.97	1	5293162.97	525.75	****
Nutrient, N	5389768.52	1	5389768.52	535.35	****
T x P	93126.65	9	10347.40	1.03	****
T x S	20509.22	3	6836.41	0.68	ns
T x N	226692.51	3	75564.17	7.51	ns
P x S	129957.11	3	43319.04	4.30	**
P x N	330919.39	3	110306.46	10.96	*
S x N	1913760.98	1	1913760.98	190.09	**
T x P x S	53379.40	9	5931.04	0.59	****
T x P x N	101976.60	9	11330.73	1.13	ns
T x S x N	62385.23	3	20795.08	2.07	ns
P x S x N	145741.28	3	48580.43	4.83	*
Error	90610.06	9	10067.78		
Total	14618880.50	63			

Appendix III M: Analysis of variance table for number of leaves at the final harvest

Source	Sum of Squares ss	Degrees of Freedom df	Mean Square ms	F	Level of Significance
Present light, T	28.2450	3	9.4150	2.32	ns
Previous light, P	46.4500	3	15.4833	3.81	ns
Species, S	280.5625	1	280.5625	69.01	****
Nutrient, N	5.2500	1	6.2500	1.54	ns
T x P	58.9850	9	6.5539	1.61	ns
T x S	17.7225	3	5.9075	1.45	ns
T x N	17.9075	3	5.9692	1.47	*
P x S	22.3350	3	7.4450	1.83	ns
P x N	4.3600	3	1.4533	0.36	*
S x N	1.5625	1	1.5625	0.38	****
T x P x S	43.3675	9	4.8186	1.19	ns
T x P x N	47.6550	9	5.2950	1.30	ns
T x S x N	24.5425	3	8.1808	2.01	ns
P x S x N	5.4275	3	1.8092	0.45	ns
Error	36.5875	9	4.0653		
Total	641.9600	63			

Appendix III N: Analysis of variance table for number of leaves shed between the first and the final harvest

Source	Sum of Squares ss	Degrees of Freedom df	Mean Square ms	F	Level of Significance
Present light, T	5.1725	3	1.7242	2.39	ns
Previous light, P	17.5025	3	5.8342	8.10	**
Species, S	0.6400	1	0.6400	0.89	ns
Nutrient, N	33.0625	1	33.0625	45.92	****
T x P	12.9425	9	1.4380	2.00	ns
T x S	1.7650	3	0.5883	0.82	ns
T x N	3.9450	3	1.3150	1.83	ns
P x S	0.7025	3	0.2342	0.33	ns
P x N	0.7125	3	0.2375	0.33	ns
S x N	0.2500	1	0.2500	0.35	****
T x P x S	2.9700	9	0.3300	0.46	ns
T x P x N	6.8025	9	0.7558	1.05	ns
T x S x N	2.5850	3	0.8617	1.20	ns
P x S x N	5.8850	3	1.9617	2.72	ns
Error	6.4800	9	0.7200		
Total	101.4175	63			

APPENDIX IV
DETAILS OF RESULTS ON ANALYSIS OF VARIANCE IN CHAPTER 5

Symbols:

ns = not significant at P < 0.05
* = P < 0.05
** = P < 0.01
*** = P < 0.001
**** = P < 0.0001

A: Net Assimilation Rate, NAR

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F	Level of Significance
R:FR ratio	5875.81	3	1958.60	29.03	***
Species	2916.40	1	2916.40	43.22	****
R:FR x Species	1264.95	3	421.65	6.25	***
Error	5397.71	80	67.47		
Total	15454.87	87			

B: Relative Growth Rate, RGR

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F	Level of Significance
R:FR ratio	1.3230	3	0.4410	31.09	****
Species	0.7324	1	0.7324	51.63	****
R:FR x Species	0.4109	3	0.1370	9.66	****
Error	1.1349	80	0.0142		
Total	3.6012	87			

C: Total Dry Weight

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F	Level of Significance
R:FR ratio	1.6503	3	0.5501	58.51	****
Species	3.1438	1	3.1438	334.38	****
R:FR x Species	0.8694	3	0.2898	30.82	****
Error	0.7521	80	0.0094		
Total	6.4156	87			

D: Height Growth

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F	Level of Significance
R:FR ratio	92.19	3	30.73	17.29	****
Species	92.24	1	92.24	51.9	****
R:FR x Species	42.09	3	14.03	7.9	****
Error	156.38	88	1.78		
Total	382.90	95			

E: Specific Stem Length, SSL

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F	Level of Significance
R:FR ratio	464527.87	3	154842.62	63.16	****
Species	648775.50	1	648775.50	264.65	****
R:FR x Species	18943.19	3	6314.40	2.58	ns
Error	196114.86	80	2451.44		
Total	1328361.41	87			

F: Internode Length

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F	Level of Significance
R:FR ratio	0.7796	3	0.2599	0.86	ns
Species	8.1984	1	8.1984	27.17	****
R:FR x Species	0.2867	3	0.0956	0.32	ns
Error	24.1433	80	0.3018		
Total	33.4079	87			

G: Number of Internodes

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F	Level of Significance
R:FR ratio	32.50	3	10.84	39.33	***
Species	100.67	1	100.67	365.43	****
R:FR x Species	11.54	3	3.84	13.96	****
Error	23.42	85	0.28		
Total	168.13	92			

H: Specific Leaf Area, SLA

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F	Level of Significance
R:FR ratio	203270.96	3	67756.99	31.44	****
Species	9723.01	1	9723.01	4.51	*
R:FR x Species	2554.82	3	851.61	0.40	
Error	172392.27	80	2154.90		
Total	387941.06	87			

I: Leaf Area Ratio, LAR

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F	Level of Significance
R:FR ratio	89791.17	3	29930.37	31.00	****
Species	1475.76	1	1475.76	1.54	ns
R:FR x Species	1055.49	3	351.83	0.36	ns
Error	77230.62	80	965.38		
Total	169552.99	87			

J: Leaf Weight Ratio, LWR

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F	Level of Significance
R:FR ratio	0.0405	3	0.0135	3.8	*
Species	0.0006	1	0.0006	0.16	ns
R:FR x Species	0.0173	3	0.0058	1.62	ns
Error	0.2846	80	0.0036		
Total	0.3430	87			

K: Stem Weight Ratio, SWR

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F	Level of Significance
R:FR ratio	0.0320	3		2.94	*
Species	0.0199	1	0.0106	5.47	*
R:FR x Species	0.0104	3	0.0199	0.96	ns
Error	0.2906	80	0.0035		
Total	0.3539	87	0.0036		

L: Root Weight Ratio, RWR

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F	Level of Significance
R:FR ratio	0.0989	3	0.0330	11.98	****
Species	0.0031	1	0.0031	1.13	ns
R:FR x Species	0.0113	3	0.0038	1.37	ns
Error	0.2202	80	0.0028		
Total	0.3335	87			

APPENDIX V
DETAILS OF RESULTS IN CHAPTER 6 ON ANALYSIS OF VARIANCE

Symbols:

ns = not significant at $P < 0.05$
* = significant at $P < 0.05$
** = significant at $P < 0.01$
*** = significant at $P < 0.001$
**** = significant at $P < 0.0001$

A: Height Increment

Source	ss	df	ms	F-value	Level of Significance
Main plots:					
Light	10548.95	3	3516.32	8.67	*
Blocks	2584.02	2	1292.01	3.19	ns
Main plot error	2432.05	6	405.34		
Sub-plots:					
Species	47213.89	3	15737.96	27.56	****
Light x Species	13222.88	9	1469.21	2.57	*
Sub-plot error	13702.82	24	570.95		
Total	89704.61	47			

B: Dry Weight at 2.7 Months

Source of Variation	ss	df	ms	F-value	Level of Significance
Main Plots:					
Light	0.111225	3	0.037075	18.40	**
Blocks					
Main plot error					
	0.027946	2	0.013973	6.94	*
	0.012086	6	0.002014		
Sub plot:					
Species					
Light x Species					
Sub-plot error					
	0.179228	3	0.059743	20.33	****
	0.171202	9	0.019022	6.47	****
	0.070537	24	0.002939		
Total	0.572224	47			

C: Dry Weight at 8.7 months

Source	SS	df	MS	F-value	Level of Significance
Main plots:					
Light	1.3869	3	0.4623	4.05	ns
Block					
Main plot error					
	0.9953	2	0.4976	4.36	ns
	0.6847	6	0.1141		
Sub-Plots:					
Sub-plots:					
Species					
Light x Species					
Sub-plot errors					
	11.8656	3	3.9552	29.99	****
	3.5322	9	0.3925	2.98	*
	3.1655	24	0.1318		
Total	21.6302	47			

D: Number of Leaves Surviving at 8.7 months

Source	SS	df	ms	F-Value	Level of Significance
Main Plots:					
Light	1545.21	3	515.07	0.61	ns
Blocks	1496.20	2	748.1	0.88	ns
Main plot error	5098.06	6	849.68		
Sub-plots:					
Species	42737.92	3	14245.97	29.20	****
Light x Species	8389.75	9	932.19	1.91	ns
Sub-plot error	11708.65	24	487.86		
Total	70975.79	47			

E: Number of Primary Branches at 5.1 months

Source	ss	df	ms	F-Value	Level of Significance
Main Plots:					
Light	76.86	3	25.62	10.26	**
Blocks	41.70	2	20.85	8.35	*
Main plot error	14.98	6	2.50		
Sub-plots:					
Species:	386.84	3	128.95	37.08	***
Light x Species	106.44	9	11.27	3.40	*
Sub-plot error	83.45	24	3.48		
Total	710.27				

F: Crown diameter at 5.1 months

Source	ss	df	ms	F-value	Level of Significance
Main Plots:					
Light	2462.04	3	820.68	4.44	ns
Blocks	6293.51	2	3146.76	17.04	**
Main plot error	1108.14	6	184.69		
Sub-plots:					
Species	46333.06	3	15444.35	36.16	*****
Light x Species	16067.93	9	1785.32	4.18	**
Sub-plot error	10251.51	24	427.15		
Total	82516.19				

APPENDIX VI
DETAILS OF RESULTS IN CHAPTER 7 ON ANALYSIS OF VARIANCE

Symbols:

ns = not significant at $P < 0.05$
* = significant at $P < 0.05$
** = significant at $P < 0.01$
*** = significant at $P < 0.001$
**** = significant at $P < 0.0001$

A. Survival

Source of variation	ss	df	ms	F-value	Level of Significance
Blocks	433.64	4	108.41	1.71	ns
Species	11339.18	3	3779.73	59.59	****
Error	761.09	12	63.42		
Total	12533.91	19			

B. Height Increment

Source of variation	ss	df	ms	F-value	Level of Significance
Blocks	1330.61	4	332.65	4.14	*
Species	2768.91	3	992.97	12.25	**
Error	904.33	12	75.36		
Total	5003.85	19			

C. Dry Weight

Source of variation	ss	df	ms	F-value	Level of Significance
Blocks	684.98	4	171.24	3.50	*
Species	1886.62	3	628.87	12.84	***
Error	587.61	12	48.97		
Total	3159.21	19			

D. Leaf Number

Source of variation	ss	df	ms	F-value	Level of Significance
Blocks	80.07	4	20.02	4.09	
Species	1391.67	3	463.89	94.70	****
Error	58.78	12	4.90		
Total	1530.52	19			